Shall We Feed Suburban Florida Scrub-Jays *Aphelocoma coerulescens*? The Importance of Human-Provided Foods on Parental Food Choice, Nestling Growth and Survival

---

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde
(Dr. sc. nat.)

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultät

der

Universität Zürich

von

Annette Sauter

von

Ermatingen TG

Promotionskomitee

Prof. Dr. Heinz-Ulrich Reyer (Vorsitz)

Dres. Karin Schiegg und Gilberto Pasinelli (Leitung)

Dr. Reed Bowman

Prof. Dr. Lukas Keller

Zürich 2005

Die vorliegende Arbeit wurde von der Mathematisch-naturwissenschaftlichen Fakultät der Universität Zürich am 15. Dezember 2005 als Dissertation angenommen.

TABLE OF CONTENTS

GENERAL INTRODUCTION

Why study the effects of human-provided foods?

With spreading worldwide urbanization an increasing number of humans live in urbanized areas and consequently, more and more plant and animal species will have to adapt to urban environments if they are to survive in the future. The conversion of wildland habitats into human-dominated landscapes, such as suburbs, villages, cities and industrials areas, strongly influences the composition of plant and animal communities. Studies on birds show that, compared to wildland communities in the same habitats, the composition of urban communities shifts because native species are replaced by human commensals. This results in lower species diversity but an increased density (e.g. Blair 1996, Clergeau et al. 1998). Consequently, urban populations often become much larger than those in wildlands (Marzluff 2001). Nevertheless, the mechanisms determining community compositions are largely unknown, because most of the conducted studies have been correlative. Understanding the mechanisms has become one of the main topics for conservation biology and is crucial for the effective management of urban species. However, the study of urbanization is not only relevant for conservation. Urbanization is a radical and rapid change in the environment and thus, represents a "natural experiment". This experiment can be used to address central questions in ecology such as how species can genetically adapt to rapid environmental changes or cope with them due to phenotypic plasticity.

In recent years, the role of behavioral mechanisms leading to extinction and successful adaptation in response to rapid environmental change has received increasing attention (Reed 1999). Sih et al. (2004) stated that limited behavioral plasticity should be a particularly important problem in human-disturbed habitats. Rapid environmental change can increase extinction risk if formerly reliable cues, on which behavioral decisions are based, are no longer associated with adaptive outcomes, thus representing evolutionary traps (Schlaepfer et al. 2002). Few examples of this phenomenon have been demonstrated in urbanized areas so far, even though urbanization probably creates many evolutionary

traps as it alters a variety of environmental cues. Dramatic examples of urbanization leading to invalid cues are Cuban treefrog (*Osteopilius septentrionalis*) and Southern toad (*Bufo terrestris*) males. They attempt to mate with dead females run over by cars, which yields no reproductive output and increases exposure to traffic. Males mate with these females because they resemble receptive females, being immobile and emitting no release calls (Meshaka 1996). On the other hand, Sol et al. (2002) found that species with greater behavioral flexibility - which they measured as the frequency of foraging innovations exhibited - are more successful invaders than less flexible species. The European blackbird, *Turdus merula*, for example, has acquired a high number of foraging innovations, shows a high phenotypic flexibility in timing of breeding and has progressively invaded urbanized areas (Sol et al. 2002, Partecke et al. 2004).

One of the most remarkable changes caused by urbanization is the availability of human-provided foods. It appears to be one of the main factors shaping urban bird communities by increasing the reproductive success of some species, but negatively affecting others (Marzluff 2001). Human-provided foods increase the availability of food and the spatial and temporal predictability of food sources (Shochat et al. 2004), and at the same time they alter the overall quality of food (Annett and Pierrotti 1999). Given these manifold changes, the effects of human-provided foods cannot always be inferred from the many food supplementation studies conducted so far (Boutin 1990). In contrast to urbanization, these experimental supplementations increase the total amount of food available for a short period but do not change the food availability year round. The food supplementation studies have shown that food availability during reproduction is one of the most important determinants of fitness in altricial birds (Martin 1987). Short-term increases in food availability can improve foraging success and can enhance growth and survival of the young. Long-term decreases in food availability can reduce the residual reproductive value of parents by lowering their survival or by impairing their subsequent production of offspring. Because foraging success influences fitness (e.g. Blanckenhorn 1991), adaptively adjusting foraging behavior to the changed food conditions in urban habitats might be vital for reproductive success.

Optimal foraging theory is based on the assumptions that foragers can adequately assess the quality and availability of all foods encountered in their environment and, hence, predicts the foraging responses to altered food availability (Berec and Krivan 2000).

However, it remains unclear whether foragers can assess the relative quality of novel food types (e.g. those provided by humans) for themselves and their young. In birds, human-provided foods often are of lower quality for nestlings than for adults (Annett and Pierrotti 1999), because most of these foods are plant-based and may be sub-optimal for nestling growth (Birkhead et al. 1999). In such cases, it should be beneficial for adult birds to avoid feeding human-provided foods to nestlings, but incorporating them into their own diet. This discrimination ought to be of greater importance in urbanized than wildland areas, because urban birds face a novel situation when feeding nestlings. At breeding, the most common food in the urbanized habitats is often human-provided, while arthropods, the most common food in the wildlands, tend to be less abundant in urbanized habitats (McIntyre 2000).

Human-provided foods are predictable in space and time, which enables urban birds to forage very efficiently (Shochat et al. 2004). It was suggested recently that the high predictability of human-provided foods leads to a different foraging and provisioning strategy in urbanized than in wildland habitats (Shochat 2004). In urbanized areas, birds could invest more in reproduction because they do not need to safeguard for periods of low food availability, i.e. living on 'credit' is affordable since the next day's income is predictable. This strategy could result in urban parents producing more but leaner young, each of which has a good chance to find sufficient food. In wildlands, birds should invest in heavier chicks, because the next income is more unpredictable. This strategy would lead to fewer young of better nutritional status that likely survive a period of low food availability, which might be caused by unfavorable weather conditions. However, Shochat (2004) did not discuss the alternative mechanism, that suburban parents might invest the additional time and energy they gain from efficient foraging into better provisioning their nestlings and therefore produce higher quality nestlings than wildland birds. In addition, food for nestlings might not be unpredictable in the wildland, because most birds raise nestlings when the natural food availability peaks (Perrins 1991) and thus, during this period the next days' food income is the highest and most predictable of the entire year. These two reasons might explain why the strategies proposed by Shochat (2004) have only been found in a few bird species. Shochat (2004) mentioned my study species, the Florida scrub-jay (*Aphelocoma coerulescens*), as a possible example of these strategies. However, foraging

and provisioning behavior of urban jays during nestling rearing have not been studied so far.

Food availability not only determines foraging success, but also influences reproductive decisions such as timing of breeding and clutch size (Martin 1987). Matching brood size to the amount of food available and temporally matching peak brood demand to the peak of food available is crucial for reproductive success (Thomas et al. 2001). Bird species could suffer from the access to human-provided foods in urban environments because, unlike the situation in their original habitat, the amount of natural food available for nestling rearing cannot be predicted from the food available before breeding, which consists of human-provided and natural foods. If birds base the decision when to breed and how many eggs to lay on the amount and quality of food available for themselves, they will overestimate the food available for nestlings, as the same foods are of lower quality for the latter. Hence, the access to human-provided foods has a high potential of leading to suboptimal reproductive decisions, if birds are not behaviorally flexible and fail to adjust their decisions to alterations in food availability. However, evidence for human-provided foods causing this mechanism is lacking so far.

Florida scrub-jays provide a unique opportunity to investigate the effects of human-provided foods on a species' reproductive success, because long-term demographic studies (Woolfenden and Fitzpatrick 1984, Bowman and Woolfenden 2001) provide detailed knowledge about the biology of this species and suggest mechanisms that can be tested experimentally. The long-term demographic studies also offer the great advantage of having access to individually color marked jays with known sex, social status, nest locations and reproductive success. In addition, we need to understand the consequences of the access to human-provided foods for the conservation of this threatened species. The Florida scrub-jay is the only bird species endemic to Florida and its population has declined by over 90% in the last century (Woolfenden and Fitzpatrick 1996). The main reason for its decline is the conversion of the native habitat into agricultural landscapes and suburbs. Today, 30% of the populations of this species live in suburbs (Breininger 1999). Most suburban populations are fed year round with *ad libitum* human-provided foods. Exposure to these foods changes timing of breeding, clutch size, and parental foraging and provisioning behavior in suburban compared to wildland populations (Bowman and Woolfenden 2001, Shawkey 2001). Furthermore, the consumption of human-provided

foods seems to reduce nestling growth and survival in suburban populations (Fleischer et al. 2003), which contributes to the decline of most suburban populations (Breininger 1999).

In my PhD thesis, I examined the consequences of reproductive decisions, which are changed by the access to human-provided foods, on nestling growth and survival (chapter 1). Further, I investigated how nestling growth and survival are affected by the inclusion of human-provided foods in the nestling diet (chapter 2). Finally, I studied the effects of the availability of human-provided foods on parental food choices, foraging and provisioning behavior (chapter 3 and 4), thus exploring the reasons of parents for feeding the low-quality human-provided foods to nestlings.

References

Annett, C. A., and R. Pierrotti. 1999. Long-term reproductive output in Western Gulls: consequences of alternate tactics in diet choice. Ecology **80**:288-297.

Berec, L., and V. Krivan. 2000. A mechanistic model for partial preference. Theoretical Population Biology **58**:279-289.

Birkhead, T. R., F. Fletcher, and E. J. Pellatt. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. Proceedings of the Royal Society of London Series B **266**:385-390.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications **6**:506-516.

Blanckenhorn, W. U. 1991. Fitness consequences of foraging success in water striders (*Gerris remigis*; Heteroptera: Gerridae). Behavioral Ecology **2**:46-55.

Boutin, R. B. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. Canadian Journal of Zoology **68**:203-220.

Bowman, R., and G. E. Woolfenden. 2001. Nest success and the timing of nest failure of Florida Scrub-Jays in suburban and wildland habitats. Pages 383-402 *in* J. M. Marzluff, R. Bowman, and R. E. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, New York.

Breininger, D. R. 1999. Florida Scrub-Jay Demography and Dispersal in a Fragmented Landscape. Auk **116**:520-527.

Clergeau, P., J. P. L. Savard, G. Mennechez, and G. Falardeau. 1998. Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. Condor **100**:413-425.

Fleischer, A. L., R. Bowman, and G. E. Woolfenden. 2003. Variation in foraging behavior, diet and the time of breeding of Florida Scrub-Jays in suburban and wildland habitats. Condor **105**:515-527.

Martin, T. E. 1987. Food as a Limit on Breeding Birds - a Life-History Perspective. Annual Review of Ecology and Systematics **18**:453-487.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19-48 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwall, MA.

McIntyre, N. E. 2000. Ecology of urban arthropods: A review and a call to action. Annals of the Entomological Society of America **94**:825-835.

Meshaka, W. E. J. 1996. Anuran Davian behavior, a darwinian dilemma. Florida Scientist **59**:74-75.

Partecke, J., T. Van't Hof, and E. Gwinner. 2004. Differences in the timing of reproduction between urban and forest European blackbirds (*Turdus merula*): result of pheontypic flexibility or genetic differences? Proceedings of the Royal Society of London Series B **271**:1995-2001.

Perrins, C. M. 1991. Tits and Their Caterpillar Food-Supply. Ibis **133**:49-54.

Reed, J. M. 1999. The role of behavior in recent avian extinctions and endangerments. Conservation Biology **13**:232-241.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology & Evolution **17**:474-480.

Shawkey, M. D. 2001. Proximate causes of brood reduction in Florida Scrub-Jays. M. Sc. thesis, University of South Florida, Tampa.

Shochat, E. 2004. Credit or debit? Resource input changes population dynamics of city-slicker birds. OIKOS **106**:622-626.

Shochat, E., S. B. Lerman, M. Katti, and D. B. Lewis. 2004. Linking optimal foraging behavior to bird community structure in an urban-desert landscape: Field experiments with artificial food patches. American Naturalist **164**:232-243.

Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution **19**:372-378.

Sol, D., S. Timmermans, and L. Levfebvre. 2002. Behavioural flexibility and invasion success in birds. Animal Behaviour **63**:495-502.

Thomas, D. W., J. Blondel, P. Perret, M. M. Lambrechts, and J. R. Speakman. 2001. Energetic and Fitness Costs of Mismatching Resource Supply and Demand in Seasonnally Breeding Birds. Science **291**:2598-2600.

Woolfenden, G. E., and J. W. Fitzpatrick. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird. Princeton University Press, Princeton, New Jersey.

Woolfenden, G. E., and J. W. Fitzpatrick. 1996. Florida Scrub-Jay *(Aphelocoma coerulescens)*. Pages 1-28 *in* A. Poole, editor. The Birds of North America. American Ornithologists' Union and The Academy of Natural Sciences, Philadelphia.

SUMMARY

Shall we feed suburban Florida scrub-jays? (*Aphelocoma coerulescens*) The importance of human-provided foods on parental food choice, nestling growth and survival

With spreading worldwide urbanization an increasing number of species are living in urbanized areas and have access to human-provided foods. The availability of human-provided foods changes the amount, quality, spatial and temporal predictability of food available. Changes in food availability between undeveloped and urban habitats are thought to be the main factor explaining differences in community compositions between these habitats. In most birds, the access to human-provided foods is associated with increased reproductive success. However, knowledge about how the access to human-provided foods changes behavioral and other mechanisms and how these mechanisms shape community composition in urban habitats is lacking.

At present, over 30% of the Florida scrub-jay (*Aphelocoma coerulescens*) populations occur in urban habitats. The species is the only bird species endemic to Florida and federally listed as Threatened. Florida scrub-jays are omnivorous with over 30% of the diet of adult birds consisting of human-provided foods. As a consequence of access to *ad libitum* human-provided foods, jays in suburban habitats breed earlier and have larger clutches than wildland birds. However, because of elevated rates of hatching failure in the suburbs, brood sizes are similar in the two habitats. After hatching, suburban birds seem to suffer from limitation in adequate food. Suburban broods are lighter and experience higher rates of brood reduction than wildland broods. Nestlings might receive less adequate food because the abundance of arthropods, the main food fed to wildland nestlings, is reduced in suburban compared to wildland habitats. In addition, suburban nestlings seem to receive food of lower quality than wildland nestlings that are fed animal foods only. We regularly observe suburban parents carrying human-provided foods to the nest, however the importance of this food type for nestling diet and growth is unknown.

In **chapter 1,** I tested if suburban nestlings grow and survive less because they are food limited. I studied variation in nestling growth and survival by supplementing suburban and wildland families with natural foods during the first 10 days after hatching of the nestlings. Suburban broods at the age of 3 days post-hatching contained equal numbers of nestlings, but had higher within-brood mass asymmetries and were heavier than wildland broods of the same age. Between 3 days and 11 days post-hatching suburban broods gained less mass than wildland broods. By 11 days post-hatching, brood masses did not differ anymore; however, food supplementation increased nestling mass and decreased brood reduction. The effect of food supplementation on mass was stronger in the suburban habitat. Post-fledging survival was lower in the suburban habitat, but was not increased by food supplementation in either habitat. Access to human-provided food advances egg laying and increases clutch sizes in suburban families, in addition it may allow suburban parents to better invest in egg quality or to better provision the nestlings at an early age. As the nestlings grow older parents seem not to meet their offspring's nutritional needs, resulting in reduced growth when compared to wildland nestlings. This is the first study showing that nestling birds in suburban habitats may be food limited even though they have access to human-provided foods. Changing food availability with urbanization may lead to mismatches between brood demands and available resources. Nevertheless, reduced fledgling survival in the suburban habitat cannot be explained only by impaired nestling growth, suggesting other impacts on the fecundity and survival of suburban nesting birds.

In **chapter 2,** I explore whether suburban nestlings are food limited because they receive plant-based human-provided foods that are of lower quality for nestling birds than animal-based foods. I expect a negative correlation between the contribution of plant foods to nestling diet and nestling mass. Because traditional methods to determine diet discrimination, such as collar rings and emetics are not applicable in this species, I evaluate the use of stable isotope analyses of nestling blood plasma to determine the contribution of plant based foods. I found that the analysis of stable isotopes is a useful tool to study diet composition in nestling birds, because it detected the diet change in experimentally provisioned nestlings. However, $\delta^{15}N$ ratios of plant-based foods were higher than expected from their trophic position, which resulted in an overlap of $\delta^{15}N$ ratios of plant-based foods and arthropods. This overlap probably prevented the calculation of the actual contribution of plant-based foods to the nestling diet. Nevertheless, I found that suburban nestlings have

a high probability of ingesting plant-based foods. The overlap might also explain why I did not find a relationship between the contribution of plant based foods to nestling diet and nestling masses.

In **chapters 3 and 4,** I investigate why parents feed human-provided foods to nestlings given the apparent costs. In chapter 3, I test experimentally whether parents do so, because 1) they do not discriminate between food types, 2) they feed the most available foods to nestlings regardless of quality, or 3) they switch to low-quality, abundant foods only when natural food availability is low. Parents discriminated between natural and human-provided foods by showing a preference for natural foods when rearing young. When availability of natural foods was experimentally decreased, parents in both habitats switched to human-provided foods. However, the switch to human-provided foods was less pronounced in suburban parents suggesting a greater preference for natural foods. Regardless of preferences demonstrated at feeders, parents in both suburbs and wildlands delivered mostly natural foods to nestlings, independent of natural food availability. However, natural foods are likely to be scarcer in the environment than in our experimental tests. Because natural food availability is lower in the suburbs than in the wildland habitat, but brood sizes are similar, parents in the suburbs may be forced to switch to human-provided foods when feeding nestlings. The results of chapter 3 suggest that time or energy limitation of the parents causes them to feed human-provided foods to nestlings. Therefore, in chapter 4, I observed parental foraging behavior in the wildland and suburban habitat to investigate whether differences in food encounter rates and parental behavior between habitats indicate food or time limitation for foraging. Because the stable isotope analyses in chapter 2 did not give conclusive results about the importance of human-provided foods for nestling diet, I also determined the importance of these foods for nestling diet in both habitats. I found no support for food or time limitation, because suburban parents were more efficient foragers than wildland parents. In addition, suburban parents took about 15% plant based foods to the nest, while wildland parents took only animal-based foods to the nests. Therefore, plant-based foods might decrease nestling growth and survival in the suburban habitat. I discuss possible mechanisms how the availability of human-provided foods can lead to the partial preference for plant-based foods observed in suburban parents despite a lack of food or time limitation for foraging.

ZUSAMMENFASSUNG

Sollen wir Buschblauhäher (*Aphelocoma coerulescens*) füttern? Die Auswirkungen anthropogener Fütterung auf die Futterwahl der Eltern und das Wachstum und Ueberleben ihrer Jungen

Die weltweite Ausdehnung der menschlichen Besiedelung hat zur Folge, dass eine immer grössere Anzahl von Menschen, Tieren und Pflanzen den gleichen Lebensraum teilen. Ausserdem führt dies auch dazu, dass sich immer mehr Tiere von anthropogenem Futter ernähren. Das anthro-pogene Futter verändert nicht nur die Menge und Qualität der verfügbaren Nahrung, sondern erhöht auch die Sicherheit, dass das Futter am vom Tier erwarteten Ort und zur erwarteten Zeit verfügbar ist. Das veränderte Futterangebot in besiedelten Habitaten wird als der wichtigste Grund zur Erklä-rung der veränderten Artenzusammensetzung zwischen unbesiedelten und besiedelten Habitaten herangezogen. Bei Vögeln weiss man, dass der Zugang zu anthropogenem Futter den Repro-duktionserfolg der meisten Arten erhöht. Aber es ist noch unklar, wie das anthropogene Futter die Verhaltens- und andere Mechanismen beeinflusst und wie diese Mechanismen die Artenzusammen-setzung in besiedelten Gebieten bestimmen.

Heute leben etwa 30% der noch verbliebenen Populationen des Buschblauhäher (Florida scrub-jay, *Aphelocoma coerulescens*) in Siedlungsräumen. Der Buschblauhäher ist die einzige endemische Vogelart Floridas. Sie ist vom Aussterben bedroht. Buschblauhäher ernähren sich omnivor. In Siedlungsräumen besteht etwa 30% der Nahrung aus anthropogenem Futter. Das anthropogene Futter verursacht, dass Häher in Siedlungsgebieten früher brüten und mehr Eier legen als Häher in unbesiedelten Gebieten. Die Brutgrössen sind jedoch in beiden Habitaten gleich, weil in besiedelten Gebieten die Schlüpfrate kleiner ist. Im Gegensatz zu ihren Eltern scheinen die Nest-linge in den Siedlungsräumen an Mangel an geeignetem Futter zu leiden. Sie wachsen weniger schnell und sterben häufiger als Nestlinge in unbesiedelten Gebieten, möglicherweise weil sie weniger und/oder schlechteres Futter erhalten. Dies könnte dadurch erklärt werden, dass die verfüg-bare Menge an natürlicher Nahrung in diesem Gebiet kleiner ist und dass die Eltern

vor allem anthropogenes Futter nutzen. Dies mag für die Eltern geeignet, für die Nestling aber von mangeln-der Qualität sein. Anthropogenes Futter ist meist pflanzlicher Natur, und Nestlinge können pflanz-liche Nahrung möglicherweise schlecht verdauen. Zudem enthält Pflanzennahrung wenig Wassser, auf welches die Jungen angewiesen sind, da sie alles Wasser über die Nahrung aufnehmen müssen. Wir beobachten, dass Nestlinge anthropogenes Futter erhalten. Aber es ist unbekannt, wie gross der Anteil des anthropogenen Futters ist und welche Auswirkungen dieses auf das Wachstum und Überleben der Nestlinge hat.

Im **ersten Kapitel** meiner Dissertation untersuche ich, ob das reduzierte Wachstums und Überleben der Nestlinge auf Futtermangel zurückzuführen ist. Dazu erhöhte ich experimentell das Insektenagebot während der ersten zehn Tage nach dem Ausschlüpfen und mass den Effekt auf das Wachstum und Überleben der Nestlinge. Ich fand, dass im Alter von drei Tagen die Bruten im be-siedelten Gebiet die gleiche Anzahl Nestlinge hatten, stärkere Grössenunterschiede zwischen dem grössten und kleinsten Nestling im Nest aufwiesen und mehr wogen als im unbesiedelten Gebiet. Danach wuchsen die Nestlinge weniger im besiedelten Gebiet, sodass sich im Alter von 11 Tagen die Brutgewichte nicht mehr unterschieden. Die Zufütterung erhöhte die Brutgewichte im Alter von 11 Tagen, verringerte die Brutreduktion in beiden Gebieten und hatte einen grösseren positiven Ein-fluss auf die Brutgewichte im besiedelten Gebiet als im unbesiedelten. Nach dem Ausfliegen war die Überlebensrate im Siedlungsgebiet kleiner, unbeinflusst von der Zufütterung. Als Folge des anthropogenen Futters scheinen die Eltern entweder mehr in die Eier oder in die frühe Jungenauf-zucht zu investieren. Später sieht es danach aus, dass die Eltern die Bedürnisse der Jungen nicht mehr decken können, wodurch deren Wachstum und Überlebensrate sinkt. Nach meinem Wissen ist dies die erste Studie, die zeigt, dass Nestlinge in Siedlungsgebieten trotz Zugang zu anthropogenem Futter in ihrem Wachstum und Überleben beeinträchtigt sind, und dass das durch die Besiedelung veränderte Futterangebot zu einem Ungleichgewicht zwischen Futterangebot und -bedürfnis der Nestlinge führen kann.

Im **zweiten Kapitel** behandle ich die Frage, ob die Nestlinge in besiedelten Räumen weni-ger stark wachsen, weil sie mehr anthropogenes Futter erhalten. Da anthropogenes Futter meist pflanzlicher Natur ist, erwarte ich eine negative Korrelation zwischen dem Anteil an pflanzlicher Nahrung, die ein Nestling aufnimmt, und dem Gewicht dieses

Nestlings. Die Nestlingsnahrung kann bei den Buschblauhähern nicht mit Hilfe traditioneller Methoden bestimmt werden, da die Eltern keine Halsringe bei ihren Jungen akzeptieren und die Verwendung von Brechmitteln bei einer bedrohten Art problematisch ist. Deshalb erprobte ich eine neue Methode zur Diätbestim-mung, die Messung von Verhältnissen stabiler Stickstoff- und Kohlenstoffisotopen in Geweben. Die experimentelle Veränderung der Nahrung führt zu einer Veränderung der Isotopenverhältnisse. Dies zeigt, dass sich die Methode dazu eignet, die Zusammensetzung der Nestlingsnahrung zu untersuchen. Unerwarteterweise überlappten die Isotopenverhältnisse der pflanzlichen Nahrung mit denen der tierischen Nahrung, weil die Isotopenwerte des Stickstoffes in der pflanzlichen Nahrung höher waren, als aufgrund der Stellung in der Nahrungskette angenommen werden konnte. Diese Überschneidung war warscheinlich der Grund dafür, dass meine Modelle eine sehr grosse Varianz für den Anteil der pflanzlichen Nahrung errechneten und dieser deshalb nur grob abgeschätzt werden konnte. Trotzdem konnte ich feststellen, dass die Nestlinge sehr wahrscheinlich pflanzliche Nahrung aufnehmen. Die Überschneidung könnte zusätzlich dazu geführt haben, dass ich keinen Zusammenhang zwischen dem Anteil an pflanzlicher Nahrung und den Nestlingsgewichten gefunden habe.

Im **dritten und vierten Kapitel** beschäftige ich mich mit den Gründen dafür, dass die Eltern anthropogenes Futter an die Jungen verfüttern, obwohl dieses minderwertig ist. Im dritten Kapitel beschreibe ich ein Experiment, in dem ich teste, ob sie dies tun, weil sie erstens die Qualität des anthropogenen Futters nicht richtig einschätzen, zweitens weil sie die am einfachsten erreich-bare Nahrung an die Jungen verfüttern oder drittens ob sie darum auf das anthropogene Futter aus-weichen, weil es zu wenig natürliches gibt. Die Eltern bevorzugten natürliches gegenüber anthro-pogenem Futter am Futtertisch. Sie unterschieden also zwischen den zwei Futtertypen. Wurde die Verfügbarkeit des natürlichen Futters am Futtertisch experimentell reduziert, wichen die Eltern aus beiden Lebensräumen vorwiegend auf anthropogenes Futter aus. Aber die Eltern im besiedelten Ge-biet nahmen immer noch mehr natürliches Futter als die Eltern im unbesiedelten Gebiet. Dies weist darauf hin, dass die Eltern im besiedelten Gebiet natürliches Futter mehr bevorzugen als die Eltern im anderen Gebiet. Unabhängig von der Wahl am Futtertisch und der Verfüg-barkeit des natürli-chen Futters in der Umgebung brachten alle Eltern fast ausschliesslich natürliches Futter zum Nest. Wahrscheinlich ist die Menge des natürlichen Futters in der Umgebung viel geringer als die Menge, die wir am Futtertisch anboten.

Deshalb erwarte ich, dass die Eltern, trotz der von mir im Experi-ment gezeigten Präferenz für natürliches Futter, im Siedlungsgebiet ge-zwungen werden auf das anthropogene Futter auszuweichen. Dies weil im besiedelten Gebiet die Eltern mit weniger natürli-chem Futter eine gleiche Anzahl an Nestlingen versorgen müssen wie im unbesiedelten Gebiet. Die Ergebnisse des dritten Kapitels weisen darauf hin, dass die Nestlinge anthropogenes Futter erhalten, weil die Eltern zu wenig natürliches Futter finden oder weil sie zu wenig Zeit für die Futtersuche verwenden können. Deshalbe untersuche ich im vierten Kapitel das Verhalten und den Erfolg der adulten Vögel bei der Futtersuche in beiden Gebieten. Weil das zweite Kapitel wenig Aufschluss über den Anteil an pflanzlichem Futter in der Nestlingsnahrung gab, bestimmte ich diesen Anteil zusätzlich. Meine Beobachtungen gaben keinen Hinweis darauf, dass die Eltern im besiedelten Ge-biet futter- oder zeitlimitiert sind. Die Eltern im Siedlungsgebiet fanden mehr anthropogene und natürliche Nahrung als die Eltern im unbesiedelten Gebiet. Trotz-dem bestand etwa 15% der Nah-rung der urbanen Nestlinge aus pflanzlichem Material, während die Nestlinge im andern Gebiet ausschliesslich tierisches Futter erhielten. Es kann also sein, dass das pflanzliche Futter ein Grund für das verringerte Wachstum und Überleben der Nestlinge im besie-delten Gebiet ist. Ich diskutiere ausserdem, welche anderen Mechanismen - ausser der Zeit- oder Futterlimitierung - die festgestellte partielle Präferenz für pflanzliche Nahrung erklären können.

ACKNOWLEDGEMENTS

First of all, I would like to thank Karin Schiegg and Gilberto Pasinelli, who involved with great enthusiasm into the adventure of accepting me as a PhD student without knowing where we would get the funding from. In addition, they encouraged and supported me in a way I could develop my own ideas and gave me great advice on how to turn my ideas into a successful research project. A special thanks to Reed Bowman who made the study possible by accepting me as a graduate intern at Archbold Biological Station, introduced me into the life of Florida scrub-jays, lead many lively discussions with me and supported me financially, logistically and with man-power. I extremely enjoyed working in his lab, having the opportunity to profit from the ongoing long-term research projects and interacting with the other interns and researchers.

Many thanks to the following people who contributed in variety of ways to this work. Uli Reyer accepted me as a PhD student and created a great working atmosphere. Glen Woolfenden taught me ornithology and how to express my thoughts clearly, let me use his study populations for foraging watches and sampled blood for and with me. Stephan Schoech gave me access to his study population, help from his coworkers, blood sample and blood processing equipment and revised my manuscripts. Jim Roth and Keith Hobson advised me for the stable isotope analyses. Jim Reynolds measured and fed birds and commented on all my manuscripts. Mark Deyrup assisted in arthropod identification. Courtney McCusker, Daniel Levitis, Artie Fleischer, Laura Kearns and Larry Riopelle contributed to the fieldwork and prevented me from going crazy during fieldwork. Jonathan W. Atwell, Kristin Bondo, Kim Brand, Miles Becker, Raoul Boughton, Kate Eldrige, Sonya LeClair, Brad Pickens, Kat Smith, Matthew Toomey, Chris Valligny and Sarah Wagner helped in the field. Archbold Biological Station and its staff provided me with everything I needed to conduct my fieldwork successfully. Uli Steiner, Martina Arioli, Christian Jakob, Andrea Weidt, Christoph Vorburger, and all other present and past members of the ecology group made life as a PhD student very enjoyable. My family, friends and flatmates in Switzerland were incredibly patient and supporting during the stormy times of my PhD.

This study would not have been possible without the financial support of

Archbold Biological Station
American Ornithologists‘ Union
Basler Stiftung für biologische Forschung
DeGiacomi Foundation
Florida Ornithological Society
Janggen-Pöhn Foundation
Roche Research Foundation
Wolfermann-Nägeli Foundation

CHAPTER 1

Suburban Florida scrub-jay nestlings suffer from food limitation despite access to ad libitum human-provided foods

Annette Sauter, Karin Schiegg and Reed Bowman

Abstract

Urbanization is increasing but its impact on animals apart from habitat loss is not well studied. Natural foods generally decline in urban areas, while human-provided foods become more abundant. We studied variation in nestling growth and survival by supplementing suburban and wildland Florida scrub–jay *(Aphelocoma coerulescens)* families with natural foods during the first 10 days after hatching of the nestlings. Suburban broods at the age of 3 days post-hatching contained equal numbers of nestlings, but had higher within-brood mass asymmetries and were heavier than wildland broods of the same age. Between 3 days and 11 days post-hatching suburban nestlings gained less mass than wildland nestlings. By 11 days post-hatching, brood masses did not differ anymore; however, food supplementation increased nestling mass and decreased brood reduction in both habitats. The effect of food supplementation on mass was stronger in the suburban habitat. Post-fledging survival was lower in the suburban habitat, but was not increased by food supplementation in either habitat. Previous studies show that access to human-provided food advances egg laying and increases clutch sizes in suburban families, in addition it may allow suburban parents to better invest in egg quality or to better provision the nestlings at an early age. As the nestlings grow older parents seem not to meet their nutritional needs, resulting in reduced growth when compared to wildland nestlings. This is the first study showing that nestling birds in suburban habitats may be food limited even though parents have access to human-provided foods. Changing food availability with urbanization may lead to mismatches between brood demands and available resources. Nevertheless, reduced fledgling survival in the suburban habitat cannot be explained only by impaired nestling growth suggesting other impacts on the fecundity and survival of suburban nesting birds.

Introduction

Food supply plays an important role in determining reproductive success in many species (Martin 1987, Boutin 1990). With accelerating worldwide urbanization, a growing number of species have access to human-provided foods. Elevated availability of food may be one of the main factors explaining the higher reproductive success of some species in urban habitats (Marzluff 2001, Prange et al. 2003), but under certain circumstances access to human-provided foods can have a negative impact on reproductive success. Some bird species might be limited in their ability to raise young, because human-provided foods are of lower quality than natural foods (Annett and Pierrotti 1999). Arthropods, the primary food fed to nestlings in many bird species (O'Connor 1984), tend to decline as a consequence of urbanization (McIntyre 2000). Nestlings depend on high quality foods to maintain their rapid growth (Birkhead et al. 1999) and declining arthropod abundance could thus lead to food limitation. Shochat (2004) suggested that as food increases so do the densities of individuals, thus potentially enhancing competition so that per capita food availability actually decreases. Hence, some species might be food-limited even if human-provided foods are of sufficient quality for successfully raising young.

Bird species could suffer from the access to human-provided foods in urban environments because, unlike the situation in their original habitat, the amount of food available before reproduction does not reflect that available during the chick-rearing phase. Adults 'decide' the timing of and investment in breeding. Food supplementation studies show that this 'decision' can depend on food availability during egg-laying (reviewed by Martin 1987, Christians 2002). Therefore, access to human-provided foods may advance laying. In many bird species across a variety of taxa, clutch size tends to decline through the breeding season (e.g. Verboven and Verhulst 1996, Winkler and Allen 1996). Thus, advancing the timing of laying could increase clutch sizes regardless of the relative quality of human-provided foods or the abundance of arthropods. Advances in laying date in response to human-provided foods can result in mismatches between resources and demands, because nestlings might be present in the nest before the seasonal peak in natural food availability. Alternatively, if arthropod abundance and the quality of human-provided foods are lower, clutch sizes might be larger than can be supported by the locally available food for young. Human-provided foods often are of lower quality for nestlings, because

most of these foods are plant-based and such foods can decrease nestling growth as found in zebra finches (*Taeniopygia guttata,* Birkhead et al. 1999). Lower reproductive success in response to experimentally advancing egg laying has been observed in blue tits *(Parus caeruleus*, Nilsson 1994), great tits (*Parus major*, Nager et al. 1997) and European kestrels (*Falco tinnunculus*, Aparicio 1998). However, no study has investigated whether advanced laying date in urban habitats leads to food limitation for nestlings. Food limitation causes increased brood reduction, i.e. the starvation of the smallest nestlings in the nest, and reduced growth and fledging masses (Lack 1954, Martin 1987). Low fledging masses have been shown to influence post-fledging survival negatively in many species (Martin 1987, Magrath 1991). Long-term studies comparing the demography of suburban and wildland populations suggest that suburban Florida scrub-jay (*Aphelocoma coerulescens*) nestlings are food-limited despite their parents' *ad libitum* access to human-provided foods (Bowman and Woolfenden 2001).

At present, over 30% of Florida scrub-jay populations occur in urban habitats. The species is the only bird endemic to Florida and federally listed as Threatened. Florida scrub-jays eat both plant and animal foods (Woolfenden and Fitzpatrick 1996). In suburban habitats over 30% of the diet of adult birds consists of human-provided foods (Fleischer 2003). As a consequence of access to *ad libitum* human-provided foods, jays in suburban habitats breed earlier and lay larger clutches than wildland birds (Bowman et al. in review). Rates of egg loss are higher in the suburbs so although clutch sizes are larger, brood sizes do not differ. Mass of suburban nestlings is lower and rates of brood reduction higher than in wildland broods (Shawkey et al. 2004). Shawkey et al. (2004) noted that per capita food delivery rates decreased with brood size in the suburbs, but not in the wildland habitat, suggesting that suburban broods were too large relative to the available resources. Suburban nestlings might receive less food because the abundance of arthropods, the main food fed to wildland nestlings (Stallcup and Woolfenden 1978), is reduced in the suburban habitat (Shawkey et al. 2004). What food they do receive might be of lower quality because human-provided foods may be substituted for arthropods. We regularly observe suburban parents taking human-provided foods to nestlings despite a preference for feeding arthropods to them, but wildland jays feed their nestlings strictly animal foods (Sauter et al. unpublished, chapter 4).

Access to human-provided foods might also influence within brood mass asymmetry. Wildland jays that were supplemented before egg-laying invested additional resources into later-laid eggs which decreased the within-brood size asymmetry relative to controls (Reynolds et al. 2003a). If suburban birds invest more in later-laid eggs because they have access to human-provided foods, within-brood asymmetries might be reduced. Alternatively, within-brood size asymmetry could be higher in the suburbs because clutches take longer to hatch than in the wildlands (Shawkey 2001), and an increased size asymmetry could represent a greater competitive disadvantage for later-hatched nestlings and, hence, facilitate brood reduction. In addition to differences in nestling growth and survival, post-fledging survival is much lower in the suburbs (Bowman, unpublished). Differences in post-fledging survival could be a residual effect of decreased fledging mass and related to food limitation or it could be a result of the different predator community that occurs in suburban habitats (Thorington 2003) or it could be some interactions between the two effects.

The goal of this study was to explore if a mismatch between food available for growing nestlings and brood demand exists in suburban habitats potentially resulting in reduced nestling growth and survival. Further, we evaluated whether differences in within-brood size asymmetries exist between habitats that might lead to decreased nestling survival. We hypothesized that because of the parents' access to human-provided foods, suburban nestlings weigh more soon after hatching and have a smaller within-brood mass asymmetry. However, because suburban adults continue to feed human-provided foods to nestlings, we expected that their growth will be slower, pre-fledging masses lighter, and brood reduction higher compared to wildland nestlings. We tested this experimentally by comparing growth and survival of supplemented and not supplemented nestlings in suburban and wildland habitats.

Materials and methods

Study organism

Florida scrub-jays are cooperative breeding birds (Woolfenden and Fitzpatrick 1996). Groups consist of a monogamous breeding pair and zero to six non-breeding helpers that defend year-round all purpose territories. Females incubate eggs and brood young. Males do not incubate or brood, but provide food to the female on the nest and to the

young. Helpers provide some food to nestlings and fledglings, and assist in nest defense. Nestlings fledge when 18 days old.

Study populations

We studied Florida scrub-jays in suburban and wildland habitats. The suburban study site was Placid Lakes Estates (27° 10'N, 81°24'W), a residential housing subdivision, near Lake Placid, Highlands County, Florida (for details see Bowman and Woolfenden 2001, 2002). In the suburban site, the native scrub vegetation occurs as patches within a matrix of roads and human housing. The wildland study site was located at Archbold Biological Station, Highlands County, Florida (for details see Mumme 1992, Schoech et al. 1996), about 11 km south of the suburban study site. In this natural preserve the scrub vegetation occurs in a heterogeneous matrix of periodically burned habitats, including xeric oak scrub, scrubby flatwoods, rosemary balds and seasonal ponds (Abrahamson et al. 1984). All birds of both populations are individually color marked and the sex, social status (breeder or non-breeder), group association, and nest status (building, incubation, brooding) of each jay is known from ongoing long-term studies on the demography of the two populations.

During the breeding season, we attempted to find all nests in every territory. All subsequent visits to the nests were done between 10 am and 3 pm because we assume predator activity is lowest at this time (Schaub et al. 1992). Nests were checked every 2 to 3 days until clutch completion to determine clutch size and onset of incubation. At both sites, just prior to the predicted hatch date, nests were checked daily until the first nestling hatched. This day was designated day 0. During the nestling period, nests were checked on days 3, 5, 8, and 11.

Food supplementation

Between March and May 2002 and 2003, we provided supplemental food to jay groups in both habitats and compared mass gain and survival of nestlings between treatment (N= 61) and control groups (N= 96). Three to zero days before hatching, feeders were placed between 10 and 20 meters from the nest and the birds were trained to retrieve peanut bits from it. The feeder consisted of a one-meter wooden pole, topped with a plastic

saucer (diameter 20 cm). Half of the groups were assigned as controls and half were supplemented; except in 2002 in the wildland, where we supplemented 10 randomly selected families only. Each day, between day 1 and 10 post-hatching, non-supplemented control groups received one peanut broken into pieces and supplemented groups received 30 grams of waxworms.

Nestling mass gain and survival

Nestlings were measured on days 3, 5, 8 and 11. On the first visit, we marked nestlings for future identification by painting a specific claw with dark red nail polish, which was reapplied on each subsequent visit. Nestlings within clutches were ranked as first, second, third etc. from the heaviest to the lightest nestling as measured on day 3. On the last visit nestlings were color banded. Nest visits after day 11 can cause premature fledging (Woolfenden and Fitzpatrick 1984).

On each visit nestlings were removed and taken at least 20 meters away from the nest to minimize disturbance at the nest. Measurements were taken according to the method used by Reynolds et al. (2003a). We weighed the nestlings (to 0.1 g) with a 100 g Pesola spring balance and measured the length of the left tarsus (to 0.05 mm) with dial calipers. To standardize measurements between researchers, two researchers measured the same nestling. New researchers were able to measure nestlings independently only when their measures lay within the measurement error of the other researcher. We measured fledging success defined as when the nest was empty and at least one young was seen alive outside of the nest, which occurs approximately 18 days post-hatching, and post-fledging survival until nutritional independence from their parents, which occurs approximately 85 days after hatching (McGowan and Woolfenden 1990).

Statistical analyses

Tarsus length and body mass were correlated at all ages ($r > 0.480$, $P < 0.001$, $N > 313$; in all cases). Therefore, we used mass as our only growth parameter. In all models food supplementation (no/yes), habitat (suburban/wildland), year (2002/2003) and the presence of helpers (no/yes) were coded as categorical variables. Other factors were continuous unless otherwise stated. Brood size was square-root transformed when used as independent variable, because brood size was bound within the range of one to five. All other transformations were done to reduce heteroscedacity of the data. Model fit was

assessed using residual plots. In all analyses, we removed non-significant interactions to build the final model. Reported values are means ± standard errors.

Nestling quality at day 3 (hypothesis 1): We predicted that shortly after hatching, suburban broods would have higher masses and a lower mass size asymmetry within broods than in the wildland. We compared mean brood masses, brood sizes and mass asymmetry between habitats. The mean brood mass per nest (log-transformed) was the dependent variable in a generalized linear model (proc glm, SAS, SAS Institute Inc. 2001). The untransformed brood size was the dependent variable in a generalized linear model with a poisson distribution and log link function (proc genmod, SAS, SAS Institute Inc. 2001). In both models, habitat, supplementation, year, presence of helpers and hatch date were the independent factors. We tested all two-way interactions. We also analyzed if a difference existed in the distribution of brood sizes between the habitats using a Pearson Chi-Square test. Broods of one nestling (N= 5) and broods of two nestlings (N= 27) as well as those with four nestlings (N= 50) and five nestlings (N= 5) were pooled, to avoid minimum expected counts lower than five. To test for variation in within-brood mass asymmetry, we used a generalized linear model (proc glm, SAS, SAS Institute Inc. 2001) on the square-root-transformed mass difference between the heaviest and the lightest nestling in the nest at day 3. Habitat, food supplementation, year, brood size, the presence of helpers and hatch date were independent variables. All two-way interactions were tested.

Food limitation of nestlings (hypothesis 2): For nestling growth we predicted that between days 3 and 11 post-hatching, (1) suburban nestlings gain less mass and that (2) smaller nestlings within broods gain less mass than larger nestlings. We expected differences with size rank of the nestling because the brood reduction mechanism predicts that if food becomes scarce, the smallest nestlings quickly starve to benefit the remainder (Lack 1968). We further predicted (3) that food supplementation would increase nestling mass gain more in the suburban than in the wildland habitat and (4) that within clutches smaller nestlings profit more from supplementation than larger nestlings, especially in the suburbs. In addition, we predicted that hatch date, number of helpers per group and brood size would influence nestling mass gain. We tested for variation in nestling mass with a generalized linear mixed model using maximum likelihood (ML) and an unstructured block for each nestling (Type=UN, proc mixed, SAS, SAS Institute Inc. 2001). The repeated subject was each nestling measured at age 3, 5, 8 and 11 days. Nestlings were 'nested'

within nests. We included age and the interactions of age with habitat, food supplementation, year, helper presence, hatch date and brood size to test the effect of these factors on nestling mass gain between day 3 and day 11 and we added the main effects of these factors to test for differences in nestling mass over all ages. We also added an interaction between size rank and food supplementation to the model, to assess whether smaller nestlings would profit more from the supplementation. The effects of food supplementation tend to be stronger when environmental conditions are poor (Nager 1997). To test for a stronger effect of food supplementation in the suburbs, where natural food availability is lower than in the wildland (Shawkey et al. 2004), we included the habitat × supplementation, age × habitat × supplementation, the year × supplementation and age × year × supplementation interactions. We included the hatch date × habitat and age × hatch date × habitat interaction to evaluate a potential effect of advanced laying in the suburban habitat.

For brood reduction until day 11 and fledging success we predicted that supplementation would have an increased effect in the suburban than in the wildland habitat. Brood reduction occurred when the lightest nestling disappeared between subsequent visits. For the brood reduction analysis, we excluded nests with complete loss of nestlings because of predation, or when nestling were lost for other reasons. We ran a generalized linear model (proc genmod, SAS, SAS Institute Inc. 2001) with either within-brood mortality (the number of nestlings lost out of number of nestlings hatched) or fledging success (no, yes) as the dependent variable. For both analyses, we used a bionimal distribution and logit link function. For within brood mortality, we added the identity of the nest as repeated subject to avoid pseudoreplication and the parameters were estimated using the GEE option. Independent variables were habitat, supplementation, year, helper presence, hatch date and all two-way interactions.

Pre-fledging masses and post-fledging survival (hypothesis 3): To test how pre-fledging masses (day 11) varied relative to habitat and food supplementation, we used the same statistical tests and independent variables as for the analyses of nestling masses and brood sizes at day 3, but we replaced the dependent variables using the nestling masses and brood sizes at day 11 instead; brood masses were not transformed. For the analyses of the distribution of brood sizes, again broods of one nestling (N= 5) and broods of two nestlings (N= 19) as well as those with four nestlings (N= 59) and five nestlings (N= 5) were pooled.

For the analysis of survival until independence, we expected that if natural foods were less abundant in suburban habitats, the heaviest nestling should be least affected and the lightest nestling the most. To avoid pseudoreplication, we used separate logistic regressions (proc logistic, SAS, SAS Institute Inc. 2001) on the heaviest and lightest nestling in the nest at day 11. Logistic regressions could be applied instead of standard survival analyses such as mark-recapture models, because dependent young do not leave their natal territory unless they die, i.e. there is no immigration or emigration until this age (Woolfenden and Fitzpatrick 1996). We incorporated only broods greater than one. Day 11 mass, habitat, food supplementation, helper presence, brood size, hatch date and rank (lightest/heaviest) were used as independent variables. We included the rank × day 11 mass, habitat × day 11 mass and habitat × supplementation interactions to test whether high masses were equally important for survival in both habitats, and the habitat × year interaction to account for habitat variation depending on year.

Results

Nestling quality at day 3 (hypothesis 1): We analyzed brood sizes and mean nestling masses in 140 broods. Consistent with our hypothesis, site had a significant effect on mean brood mass ($F_{1,135}$=27.80, P < 0.001, Figure 1); the mean brood mass on day 3 was greater in the suburbs. Brood size did not differ between sites (χ^2 =0.05 P =0.826) and food supplementation did not influence brood size (χ^2 =0.36, P =0.547) or mean brood mass ($F_{1,135}$= 0.86, P = 0.354). In addition, neither brood size nor mean brood mass varied between years (χ^2 =0.16, P =0.685, $F_{1,135}$= 1.39, P = 0.240 respectively) and depended on helper presence (χ^2 = 0.04, P= 0.850, $F_{1,135}$= 1.16, P= 0.284 respectively). Brood size did not differ with hatching date (χ^2 =0.23, P= 0.632), but mean brood mass tended to increase with hatching date ($F_{1,135}$= 3.21, P = 0.075). The deviance for the brood size model was 40.109. The distribution of brood sizes did not differ between habitats either (χ^2 =1.826, df=2, P =0.401). In summary, only site influenced brood mass, and none of the variables tested influenced brood size.

Contrary to our prediction, within-brood mass asymmetry was greater in the suburbs than the wildlands ($F_{1,125}$= 6.26, P = 0.014, Figure 2). Neither food supplementation ($F_{1,125}$= 0.08, P= 0.775), year ($F_{1,125}$= 0.31, P= 0.579) nor helper presence ($F_{1,125}$= 1.89, P= 0.172) influenced within-brood mass asymmetry. However, within-brood

mass asymmetry decreased with the presence of helpers in the suburbs (without 2.48 ± 0.07 g, with helpers 2.12 ± 0.11 g), but increased with the presence of helpers in the wildlands (without 2.10 ± 0.06 g, with helpers 2.29 ± 0.06 g, habitat × helper: $F_{1,125}$=16.28, P< 0.001). Mass asymmetry did not vary with brood size in the wildland, except for the rare broods of five (Figure 2). Mass asymmetry increased with each additional nestling in the brood in the suburban habitat (brood size × habitat, $F_{1,125}$= 7.45, P= 0.007), explaining the increase of mass asymmetry with brood size ($F_{1,125}$= 27.74, P < 0.001). Mass asymmetry tended to increase with hatching date ($F_{1,125}$= 3.44, P =0.066). The overall model for the mass asymmetry was significant ($F_{8,125}$=7.87, P < 0.001).

Food limitation of nestlings (hypothesis 2): Mass gain between day 3 and 11 followed most of our predictions (Table 1, Figure 3). Mass gain was lower in the suburban than in the wildland habitat and was lower for nestlings ranking low in the size hierarchy at day 3 than for nestlings high in the size hierarchy. Supplementation increased mass gain more in the suburban than the wildland habitat. However, supplementation did not have a stronger effect on mass gain of nestlings ranking low in the size hierarchy. Furthermore, mass gain was higher in 2002 than in 2003, and it increased with decreasing brood size, but did not vary with hatch dates.

For brood reduction and fledging success we found similar results. Both were higher in the suburban than in the wildland habitat (Table 2, Figure 3). Food supplementation decreased both factors, but contrary to our expectation the effect was not greater in the suburban habitat than in the wildland. A significant interaction existed between supplementation and year; supplementation reduced brood reduction rate and increased fledging success only in 2003; however, both factors did not differ between years and no significant interaction between habitat and year existed. Helper presence influenced neither of the factors. In addition, brood reduction but not fledging success increased with hatching date.

Pre-fledging masses and post-fledging survival (hypothesis 3): We analyzed the brood size and pre-fledging brood mass of 109 broods measured 11 days post-hatching (Figure 1). Neither the total brood size (χ^2 = 0.090, P= 0.761) nor mean brood mass ($F_{1,102}$= 2.22,P= 0.150) differed significantly between habitats. The supplementation did not influence brood sizes (χ^2 = 0.05, P = 0.821), but increased mean brood masses ($F_{1,102}$= 8.61, P= 0.004); however the interaction between supplementation and habitat was not

significant. Brood sizes (χ^2 = 1.65, P= 0.198) did not differ between years, but mean brood masses ($F_{1, 102}$= 5.19, P= 0.025) were higher in 2002 than in 2003. Brood sizes and mean brood masses did not depend on the presence of helpers (χ^2 = 0.94, P= 0.332, $F_{1, 101}$= 0.11, P= 0.738 respectively), nevertheless, mean brood mass increased more with helper presence in the suburban than the wildland habitat (habitat x helper presence, $F_{1, 101}$= 4.71, P= 0.032). Brood sizes (χ^2 = 0.59, P= 0.444) and mean brood masses ($F_{1, 101}$= 0.95, P= 0.332) did not depend on hatching date. The deviance for the brood size model was 38.894. In contrast to the distrubution of brood sizes at day 3, the distribution of brood sizes at day 11 differed significantly between habitats (χ^2 = 8.401, df= 2, P= 0.015). Compared to the wildland, in the suburban habitat the proportion of broods with less than three nestlings was similar (suburban 36%, wildland 40%), the proportion of broods with three nestlings was higher (suburban 46 %, wildland 22 %) and the proportion of broods with more than three nestlings was smaller (suburban 18%, wildland 37%).

The probability of surviving to independence was associated with different factors for the heaviest and the lightest nestlings in the nests at day 11 (Table 3). Contrary to our expectations, supplementation did not increase the survival of the heaviest or the lightest nestling, nor was there a stronger effect in the suburban than the wildland habitat. In addition, the lightest nestlings were more likely to survive if they attained higher day 11 masses and when helpers were present. While the probability of survival of the lightest nestlings did not differ between the habitats, the heaviest nestlings were more likely to survive in the wildland than the suburban habitat. In the suburban habitat, heaviest nestlings had a higher probability of surviving to independence if they attained higher day 11 masses, but the survival of the heaviest nestlings in the wildland was independent of their day 11 mass (habitat x day 11 mass, Table 3). Overall, the survival of the heaviest nestlings did not relate to its day 11 mass.

Discussion

We have demonstrated that nestling Florida scrub-jays raised in suburban habitats suffer from food limitation even though their parents have access to human-provided foods. We found that: (1) suburban parents produced a similar number of nestlings but of higher mass early in the nestling phase than do wildland parents; (2) suburban nestlings gained less mass, experienced more brood reduction and lower fledging success; and (3) lower pre-

fledging masses affected fledgling mortality in both habitats. Our hypothesis that food limitation causes reduced growth and survival was supported because food supplementation increased nestling growth and decreased brood reduction and the effect on nestling growth was stronger in the suburban habitat.

Nestling quality at day 3: The higher mean brood mass of suburban nests at day 3 is consistent with the hypothesis that human-provided food is of relatively high quality for adults. Like wildland females that are provided high-quality supplemental foods (Reynolds et al. 2003b), suburban females appear to be able to invest additional resources in the quality of their eggs or young. Heavier masses of suburban nestlings at day 3 relative to wildland birds could result from eggs of higher quality (Nisbet 1978, Stokland and Amundson 1988) or from better provisioning by the parents. Because food supplementation had no effect on nestling mass at this age, we think that increased masses result from eggs of higher quality. Before breeding, females in the suburbs have higher levels of plasma protein than suburban females, possibly because they have easy access to protein-rich human-provided foods (Schoech and Bowman 2003) during a time when natural foods for jays are likely at their annual nadir. Plasma protein levels reflect the level of vitellogenin production prior to egg laying and the bulk of the yolk protein is derived from vitellogenin (White 1991), suggesting that suburban females invest more in egg quality than do wildland females.

Contrary to our predictions, day 3 nestling mass asymmetry within broods was higher in the suburban than in the wildland habitat. Within-brood mass asymmetry may result from variation in egg size, in hatching interval, or in parental investment immediately after hatching (Nilsson 1993, Stoleson and Beissinger 1995, Smiseth et al. 2003). Because food for nestlings is more limiting in the suburbs than in the wildlands, suburban parents might be more likely to apply a brood reduction strategy, i.e. the smallest nestlings receive the least food (Royle 2000), which could explain a higher mass asymmetry within nests. However, food supplementation did not affect nestling masses at this age. Alternatively, Shawkey (2001) found that within-brood hatching spread was significantly longer in the suburbs than in the wildlands, potentially leading to greater within-brood mass asymmetry. The hatching interval may be longer because suburban clutches are larger than wildland clutches and it takes larger clutch sizes longer to hatch (e.g. Wellicome 2005). We found that mass asymmetry increased with brood size in the suburbs, but not in the wildlands. In

the latter, only in broods of five was the mass asymmetry higher than in smaller broods and broods of five are rare. Therefore, the difference in clutch size between the habitats cannot explain the variation in mass asymmetry. Other differences between suburban and wildland habitats may interact with brood size causing the observed difference in size asymmetry. The increased hatching interval could also be explained by other factors we have not quantified in this study such as variation in the lengths of laying interval, in egg sizes, in the onset of incubation, in incubation efficiency and in ambient temperatures (Slagsvold 1986, Eikenaar et al. 2003).

Food limitation of nestlings: Suburban nestlings were more food-limited than wildland nestlings. Between days 3 and 11, suburban nestlings gained less mass and survived less frequently than wildland nestlings, as indicated by the elevated rate of brood reduction and reduced fledging success. Higher predation rates in the suburban than the wildland habitat (Thorington 2003) could lower suburban fledging success more, but the consistency of the results of within brood mortality and fledging success suggests that variation in fledging success between the habitats is mainly explained by starvation. In groups experimentally provisioned with arthropods, nestling mass gain and survival increased in both habitats, and the effect of the supplementation on nestling mass gain was stronger in the suburbs than the wildland. Surprisingly, this interaction did not exist for brood reduction and fledging success, in part because of the different response of suburban broods to supplementation in 2002 and 2003. Food supplementation is expected to be more effective when background food availability is low (e.g. Korpimäki 1989, Boutin 1990, but see Massemin et al. 2002). We think that background food levels were lower in 2003 than in 2002, because in 2003 control broods gained less mass and mean brood masses at day 11 were lower in both habitats. Accordingly, supplementation decreased brood reduction in the suburban habitat more in 2003 than in 2002. This finding suggests that food limitation partly explains the high rate of brood reduction in the suburban relative to the wildland habitat. In the latter, brood reduction is relatively rare (Shawkey et al. 2004) and food supplementation is not likely to have any effect except in years in which food is limited. In contrast to this study, Reynolds et al. (2003a) found that supplementation increased fledging success, but had no effect on day 11 masses and the effect did not differ between years of different natural food availability in the wildland population. However, these results might not be directly comparable with ours because Reynolds et al. (2003a) used

artificial diets as supplemental food, which might be less easily digestible than arthropods used in our study. Differences in hatch date, brood size, within-brood asymmetry and helper presence between the habitats could explain differences in mass gain, brood reduction, and fledging success. The latter three variables were independent of hatching date in both habitats. Thus, the differences in nestling masses and survival until fledging between suburban and wildland habitats are not consistent with earlier breeding in the suburbs (Bowman and Woolfenden 2001, Bowman et al. in review) which could have led to a temporal mismatch between the peak of natural food availability and peak brood demand. Brood size at day 3 did not differ between habitats, so brood size effects are not likely to lead to habitat-specific differences in growth or survival. However, although brood sizes do not differ between the habitats, the mean brood size in the suburbs might be larger than the environment can support given the reduced abundance of arthropods (Shawkey et al. 2004) and the relatively poor-quality of human-provided foods for growing nestlings. In support, brood reduction was more intense in the suburban habitat also when brood size was included in the model. Our results agree with studies on blue tits *(Parus caeruleus)* showing that populations in poor habitats are more susceptible to mismatches between brood sizes and resources than in good habitats (Tremblay et al. 2003, 2005). In addition, the larger within-brood mass asymmetry in the suburbs could exacerbate differences in the rates of brood reduction between the two habitats, because nestling asymmetry increases the differences in competitiveness of nestlings in the nest (Lack 1954, Valkama 2002). The presence of helpers had a positive effect on both nestling mass and rates of brood reduction, as found in a previous study on the same populations (Shawkey et al. 2004), but not on fledging success. Thus, the lack of helpers in the suburban habitat seems another factor contributing to decreased nestling growth and survival compared to the wildland. Even though we have demonstrated that suburban nestlings suffer from food limitation, it remains to be studied whether a reduced amount of food or a diet of inferior quality causes food limitation.

Pre-fledging masses and post-fledging survival: Suburban nestlings did not attain significantly lower masses 11 days post-hatching than wildland nestlings in this study, in contrast to the longterm demographic studies finding lower suburban than wildland masses at this age (Bowman, unpublished data). The mass difference was probably not statistically significant because the supplementation decreased the difference between the suburban and

the wildland habitat increasing the suburban masses more than the wildland masses and because in 2002, when natural food availability seemed to be high in both habitats, also the control nestlings attained similar masses in the suburban and wildland habitat. Nevertheless, we expect that the suburban nestlings fledged with lighter masses, because they probably continued to grow less than wildland nestlings between our measures at day 11 and fledging at day 18. In addition, the survival analyses support the hypothesis that lower post-fledging survival of suburban nestlings is associated with lower pre-fledging masses. In both habitats, post-fledging survival of the lightest nestlings was influenced by day 11 mass, post-fledging survival of the heaviest nestlings depended on a greater extent on day 11 mass in the suburban than in the wildland habitat. Nevertheless, impaired nestling growth did not explain the reduced post-fledging survival in the heaviest nestlings in the suburban compared to the wildland habitat. Food limitation, predation risk or road mortality during the post-fledging period are habitat differences that might influence post-fledging survival we have not quantified in this study. The impact of food limitation should decrease because the digestive efficiency for carbohydrate foods increases when nestlings age (Caviedes-Vidal and Karasov 2001). We hence expect higher post-fledging predation rates in the suburban than in the wildland habitat. Avian and mammal predators tend to be more abundant in our suburban area (Thorington and Bowman 2003) and in other urbanized areas (Blair 1996) compared to the wildlands. Mortality of young birds along roads also could be high in the suburbs. We have found suburban fledglings killed by cars (Sauter and Bowman, pers. observation) and evidence exists that post-fledging survival in wildland territories along roads is affected by road mortality (Mumme et al. 2000). We also showed that post-fledging survival of the lightest nestlings depended on the presence of helpers. This finding supports the role of food limitation for post-fledging survival of the lightest nestlings, because helpers contribute to fledgling feeding (McGowan and Woolfenden 1990).

General conclusions: In summary, we have found a new mechanism explaining impaired reproductive success in species living in urbanized areas. Access to human-provided foods causes a mismatch between brood demand and resources available for broods. While this mechanism might be confined to species where nutritional needs differ between adults and young, such as many bird species, urbanization likely changes a wide range of environmental cues on which adaptive behavior is based. Therefore, urbanization

may have a high potential to affect species with limited phenotypic variation (Sih et al. 2004). Thomas et al. (2001) found that a fixed response to photoperiod led to a mismatch between prey abundance and nestling demand in blue tits. Florida scrub-jays seem to have a fixed response to the amount of food available; suburban birds with *ad libitum* access to human-provided foods breed earlier and vary their timing of breeding less than wildland jays with fluctuating natural food availability. Consequently, suburban birds lay larger clutches (Bowman et al. in review). However, the mismatch and the resulting food limitation seem to contribute little to the reduced reproductive success found in our suburban population. In our study, habitat differences influenced post-fledging survival more strongly than they reduced nestling mass. In addition, the costs of laying additional eggs and producing higher quality offspring at hatching may be low. In contrast to suburban nestlings, suburban parents do not experience food limitation in the presence of human-provided foods. Furthermore, the high mass asymmetry among nestlings may allow parents to reduce brood size rapidly further minimizing the costs of producing too many young. Smith et al. (1995) and Bize et al. (2002) found that it is beneficial to increase investment in egg quality during inferior environmental conditions but not under good conditions. Therefore, as long as the costs are low, it might be the-best-of-a-bad-job to produce high quality hatchlings even though several of them will not survive.

Acknowledgements

We thank numerous research assistants, students and interns that helped in the field, especially J.W. Atwell, R. Boughton, A. Fleischer, B. Pickett, C. McCusker and J. Reynolds. S. J. Schoech gave us access to his study population. This manuscript benefited from the comments of S. J. Reynolds and the statistical advice of U. Steiner and L.F. Keller. Research in the suburban and wildland sites was supported by NSF grants IBN-0077469 and -0346557 to RB and grants IBN-9983201, -0235821, and -0346328 to Stephan J. Schoech. All research on this listed species was permitted by the US Fish and Wildlife Service (permit TE824723-5 to R. Bowman).

References

Abrahamson, W. G., A. F. Johnson, J. N. Layne, and P. A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. Florida Scientist **47**:209-250.

Annett, C. A., and R. Pierrotti. 1999. Long-term reproductive output in Western Gulls: consequences of alternate tactics in diet choice. Ecology **80**:288-297.

Aparicio, J. M. 1998. Individual optimization may explain differences in breeding time in the European kestrel *Falco tinnunculus*. Journal of Avian Biology **29**:121-128.

Beissinger, S. R., and J. R. Waltman. 1991. Extraordinary Clutch Size and Hatching Asynchrony of a Neotropical Parrot. Auk **108**:863-871.

Birkhead, T. R., F. Fletcher, and E. J. Pellatt. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. Proceedings of the Royal Society of London Series B **266**:385-390.

Bize, P., A. Roulin, and H. Richner. 2002. Covariation between egg size and rearing condition determines offspring quality: an experiment with the alpine swift. Oecologia **132**:231-234.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications **6**:506-516.

Boutin, R. B. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. Canadian Journal of Zoology **68**:203-220.

Bowman, R., and G. E. Woolfenden. 2001. Nest success and the timing of nest failure of Florida Scrub-Jays in suburban and wildland habitats. Pages 383-402 *in* J. M. Marzluff, R. Bowman, and R. E. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, New York.

Bowman, R., and G. E. Woolfenden. 2002. Nest site selection by Florida Scrub-Jays in natural and human-modified habitats. Wilson Bulletin **114**:128-135.

Bowman, R., G. E. Woolfenden, and J. W. Fitzpatrick. In review. Sources of variation in the timing of reproduction between urban and wildland Florida scrub-jays. Ecological Applications

Caviedes-Vidal, E., and W. H. Karasov. 2001. Developmental changes in digestive physiology of nestling house sparrows, *Passer domesticus*. Physiological and Biochemical Zoology **74**:769-782.

Christians, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. Biological Reviews of the Cambridge Philosophical Society **77**:1-26.

Eikenaar, C., M. L. Berg, and J. Komdeur. 2003. Experimental evidence for the influence of food availability on incubation attendance and hatching asynchrony in the Australian reed warbler *Acrocephalus australis*. Journal of Avian Biology **34**:419-427.

Fleischer, A. L., R. Bowman, and G. E. Woolfenden. 2003. Variation in foraging behavior, diet and the time of breeding of Florida scrub-jays in suburban and wildland habitats. Condor **105**:515-527.

Korpimäki, E. 1989. Breeding performance of Tengmalm's owl *Aegolius funereus*: effects of supplementary feeding in a peak vole year. Ibis **131**:268-283.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Magrath, R. D. 1991. Nestling Weight and Juvenile Survival in the Blackbird, *Turdus merula*. Journal of Animal Ecology **60**:335-351.

Martin, T. E. 1987. Food as a Limit on Breeding Birds - a Life-History Perspective. Annual Review of Ecology and Systematics **18**:453-487.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19-48 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwall, MA.

Massemin, S., E. Korpimäki, V. Pöyri, and T. Zorn. 2002. Influence of hatching order on growth rate and restling metabolism of kestrel nestlings. Journal of Avian Biology **33**:235-244.

McGowan, K. J., and G. E. Woolfenden. 1990. Contributions to fledgling feeding in the Florida scrub jay. Journal of Animal Ecology **59**:691-707.

McIntyre, N. E. 2000. Ecology of urban arthropods: A review and a call to action. Annals of the Entomological Society of America **94**:825-835.

Mumme, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. Behavioral Ecology and Sociobiology **31**:319-328.

Mumme, R. L., S. J. Schoech, G. E. Woolfenden, and J. W. Fitzpatrick. 2000. Life and death in the fast lane: Demographic consequences of road mortality in the Florida Scrub-Jay. Conservation Biology **14**.

Nager, R. G., C. Ruegger, and A. J. VanNoordwijk. 1997. Nutrient or energy limitation on egg formation: A feeding experiment in great tits. Journal of Animal Ecology **66**:495-507.

Nilsson, J. Å. 1994. Energetic bottle-necks during breeding and the reproductive costs of beeing too early. Journal of Animal Ecology **63**:200-208.

Nilsson, J. Å. 1993. Energetic constraints on hatching asynchrony. American Naturalist **114**:158-166.

Nisbet, I. C. T. 1978. Dependence of fledging success on egg size, parental performance and egg composition among Common and Roseate Terns, *Sterna hirundo* and *S. dougallii*. Ibis **120**:205-215.

O'Connor, R. J. 1984. The growth and development of birds. John Wiley & Sons, Chichester.

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. Journal of Wildlife Management **67**:324-333.

Reynolds, S. J., S. J. Schoech, and R. Bowman. 2003a. Diet quality during prelaying and nestling periods influences growth and survival of Florida scrub-jay *Aphelocoma coerulescens* chicks. Journal of Zoology **261**:217-226.

Reynolds, S. J., S. J. Schoech, and R. Bowman. 2003b. Nutritional quality of prebreeding diet influences breeding performance of the Florida scrub-jay. Oecologia **134**:308-316.

Royle, N. 2000. Overproduction in the Lesser Black-backed Gull - can marginal chicks overcome the initial handicap of hatching asynchrony? Journal of Avian Biology **31**:335-344.

Schaub, R., R. L. Mumme, and G. E. Woolfenden. 1992. Predation on the Eggs and Nestlings of Florida Scrub Jays. Auk **109**:585-593.

Schoech, S. J., and R. Bowman. 2003. Does differential access to protein influence differences in timing of breeding of Florida Scrub-Jays (*Aphelocoma coerulescens*) in suburban and wildland habitats? Auk **120**:1114-1127.

Schoech, S. J., R. L. Mumme, and J. C. Wingfield. 1996. Prolactin and helping behaviour in the cooperatively breeding Florida scrub-jay, *Aphelocoma c. coerulescens*. Animal Behaviour **52**:445-456.

Shawkey, M. D. 2001. Proximate causes of brood reduction in Florida Scrub-Jays. M. Sc. thesis. University of South Florida, Tampa.

Shawkey, M. D., R. Bowman, and G. E. Woolfenden. 2004. Why is brood reduction in Florida Scrub-jays higher in suburban than in wildland habitats? Canadian Journal of Zoology **82**:1427-1435.

Shochat, E. 2004. Credit or debit? Resource input changes population dynamics of city-slicker birds. OIKOS **106**:622-626.

Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution **19**:372-378.

Slagsvold, T. 1986. Asynchronous versus synchronous hatching in birds: experiments with the pied flycatcher. Journal of Animal Ecology **55**:1115-1134.

Smiseth, T., R. J. Bu, A. K. Eikenaes, and T. Amundson. 2003. Food limitation in asynchronous bluethroat broods: effects on food distribution, nestling begging, and parental provisioning rules. Behavioral Ecology **14**:793-801.

Smith, H. G., T. Ohlsson, and K.-J. Wettermark. 1995. Adaptive significance of egg size in the European starling: experimental tests. Ecology **76**:1-7.

Stallcup, J. A., and G. E. Woolfenden. 1978. Family status and contributions to breeding by Florida Scrub Jays. Animal Behaviour **26**:1144-1156.

Stokland, J. N., and T. Amundson. 1988. Initial size hierachy in broods of the Shag: relative significance of egg size and hatching asynchrony. Auk **105**:308-315.

Stoleson, S., and S. R. Beissinger. 1995. Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period? Current Ornithology **12**:191-270.

Thomas, D. W., J. Blondel, P. Perret, M. M. Lambrechts, and J. R. Speakman. 2001. Energetic and Fitness Costs of Mismatching Resource Supply and Demand in Seasonnally Breeding Birds. Science **291**:2598-2600.

Thorington, K. K., and R. Bowman. 2003. Predation on artificial nests increases with human housing density in suburban habitats. Ecography **26**:188-196.

Tremblay, I., D. W. Thomas, J. Blondel, P. Perret, and M. M. Lambrechts. 2005. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits *Parus caeruleus*. Ibis **17-24**.

Tremblay, I., D. W. Thomas, M. M. Lambrechts, J. Blondel, and P. Perret. 2003. Variation in Blue Tit breeding performance across gradients in habitat richness. Ecology **84**:3033-3043.

Valkama, J., E. Korpimäki, A. Holm, and H. Hakkarainen. 2002. Hatching asynchrony and brood reduction in Tengmalm's owl *Aegolius funereus*: the role of temporal and spatial variation in food abundance. Oecologia **133**:334-341.

Verboven, N., and S. Verhulst. 1996. Seasonal variation in the incidence of double broods: The date hypothesis fits better than the quality hypothesis. Journal of Animal Ecology **65**:264-273.

Wellicome, T. I. 2005. Hatching asynchrony in Burrowing Owls is influenced by clutch size and hatching success but not by food. Oecologia **142**:326-334.

White, H. B. I. 1991. Maternal diet, maternal proteins and egg quality. Pages 1.15 *in* C. D. Deeming and M. W. J. Ferguson, editors. Egg incubation: its effects on embryonic development in birds and reptiles. Cambridge University Press, Cambridge, United Kingdom.

Winkler, D. W., and P. E. Allen. 1996. The seasonal decline in tree swallow clutch size: Physiological constraint or strategic adjustment? Ecology **77**:922-932.

Woolfenden, G. E., and J. W. Fitzpatrick. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird. Princeton University Press, Princeton, New Jersey.

Woolfenden, G. E., and J. W. Fitzpatrick. 1996. Florida Scrub-Jay *(Aphelocoma coerulescens)*. Pages 1-28 *in* A. Poole, editor. The Birds of North America. American Ornithologists' Union and The Academy of Natural Sciences, Philadelphia.

Table 1: Results of a maximum likelihood mixed model analysis of potential factors affecting nestling mass at days 3, 5, 8 and 11 (N= 283 nestlings, -2 log likelihood =7166.1, likelihood-ratio test= 1524.74, df= 9, P< 0.001). Age and interactions terms with age test for differences in mass gain among nestlings. Main effects test for differences in masses over all ages among nestlings

Source	F	df	P
Age	36.81	1	< 0.001
Age × habitat (suburban, wildland)	3.90	1	0.050
Age × supplementation (no, yes)	34.24	1	< 0.001
Age × year (2002, 2003)	9.69	1	0.002
Age × helper presence (no, yes)	3.28	1	0.072
Age × brood size	3.38	1	0.068
Age × hatch date	0.12	1	0.734
Age × size rank at day 3	7.95	4	< 0.001
Age × supplementation × habitat	4.08	1	0.045
Habitat (suburban, wildland)	0.60	1	0.434
Supplementation (no, yes)	0.11	1	0.737
Year (2002, 2003)	0.52	1	0.473
Helper (no, yes)	0.04	1	0.836
Brood size	0.98	1	0.324
Hatch date	6.80	1	0.010
Size rank at day 3	5.63	4	< 0.001
Nestling (nest)	9.10	99	< 0.001

Table 2: Generalized linear model of potential factors predicting brood reduction: within brood mortality (number of nestlings lost out of number of nestlings hatched) until day 11 (N=101 nests, deviance= 89.073) and the probability of fledging success (N= 151 nests, deviance= 191.696).

		Within brood mortality until day 11				Probability of fledging success			
Parameter	df	Estimate	SE	Chi-Square	P	Estimate	SE	Chi-Square	P
Intercept	1	-4.164	1.507	7.63	0.006	2.498	1.752	2.03	0.154
Habitat (suburban, wildland)	1	1.574	0.485	10.53	0.001	-1.118	0.364	10.64	0.001
Supplementation (no, yes)	1	0.955	0.483	3.91	0.048	-0.877	0.507	2.99	0.084
Year (2002, 2003)	1	-0.129	0.567	0.05	0.820	-0.482	0.552	0.76	0.383
Helper (no, yes)	1	1.224	0.453	7.29	0.007	-0.436	0.361	1.46	0.228
Hatch date	1	0.001	0.014	0.01	0.918	0.065	0.662	1.05	0.306
Brood size at hatching	1					-0.012	0.011	0.01	0.921
Year × supplementation	1	-2.019	0.884	5.21	0.022	1.409	0.712	3.86	0.050

Table 3: Logistic model of independence (yes/no) depending on year, site, supplementation, helper presence brood size and hatch date of the heaviest and lightest chick in the nest. The probability of reaching independence was modeled (heaviest:-2 log likelihood= 149.386, likelihood-ratio test= 21.227, df= 8, P= 0.007; lightest: -2 log likelihood= 132.948, likelihood-ratio test= 24.744, df= 7, P< 0.001)

		heaviest (N = 108)				lightest (N=108)			
Effect	df	Estimate	SE	Chi-Square	P	Estimate	SE	Chi-square	P
Intercept	1	2.062	3.082	0.447	0.504	-1.324	3.105	0.182	0.670
day 11 mass	1	0.032	0.038	0.7466	0.388	0.102	0.032	10.163	0.001
habitat (suburban, wildland)	1	-4.899	1.774	7.626	0.006	-0.322	0.257	1.564	0.211
supplementation (no, yes)	1	0.263	0.238	1.219	0.270	0.419	0.266	2.482	0.115
year (2002, 2003)	1	0.098	0.223	0.194	0.660	-0.108	0.245	0.195	0.659
helper (no, yes)	1	-0.401	0.227	3.109	0.078	-0.512	0.247	4.2995	0.038
brood size	1	-0.277	0.781	0.126	0.618	-0.167	0.273	0.372	0.542
hatch date	1	-0.032	0.018	3.092	0.079	-0.029	0.021	1.973	0.160
day 11 mass x habitat	1	0.097	0.037	6.847	0.009				

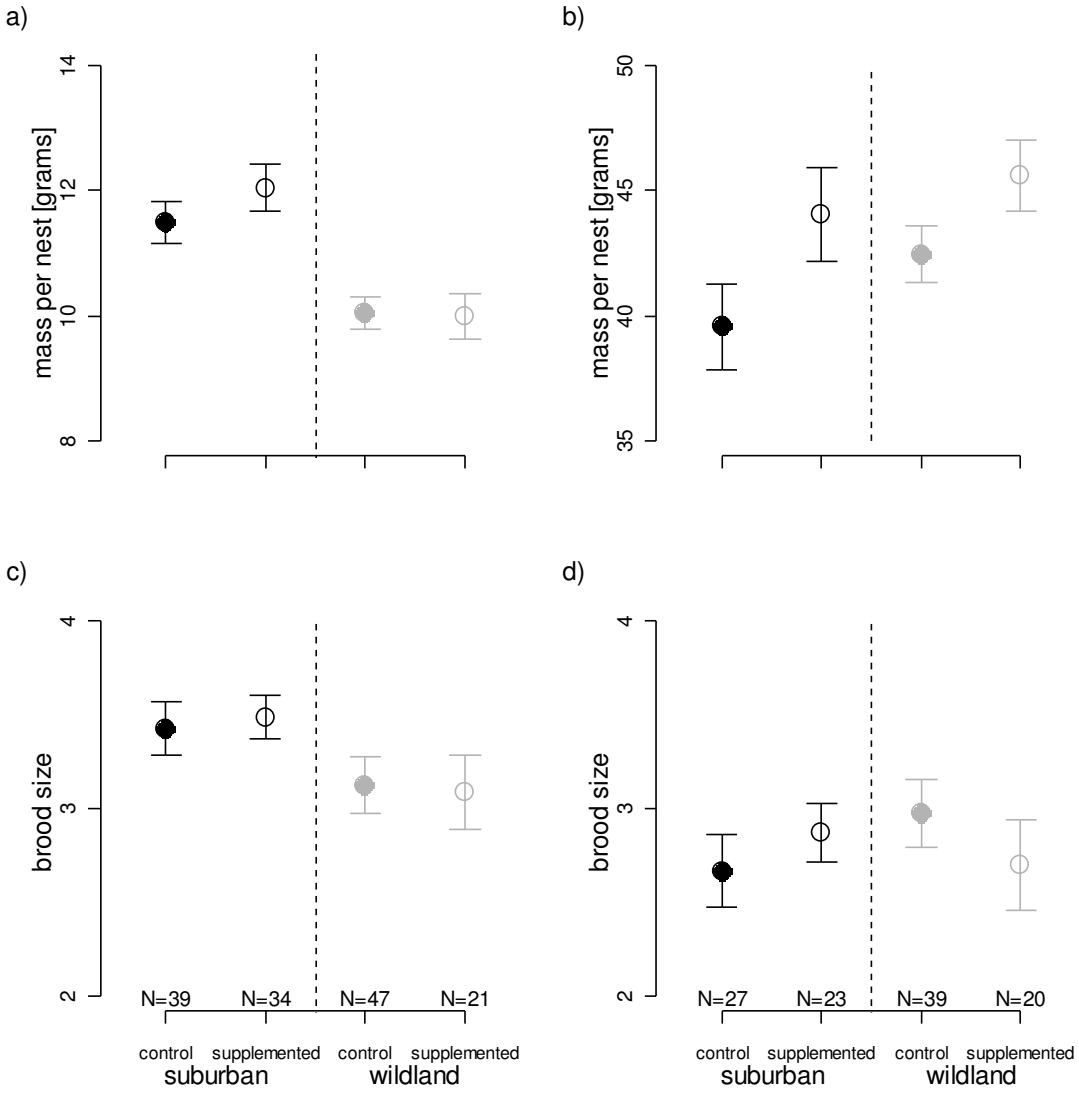

Figure 1: Mean brood mass ± SE of nestlings (a + b) and brood sizes ± SE (c + d) at at day 3 (a + c) and day 11 (b + d) in the suburban habitat (black circles) and wildland habitat (gray circles) in control nests (closed circles) and supplemented nests (open circles) both years combined. Note different scaled axes. N= number of nests.

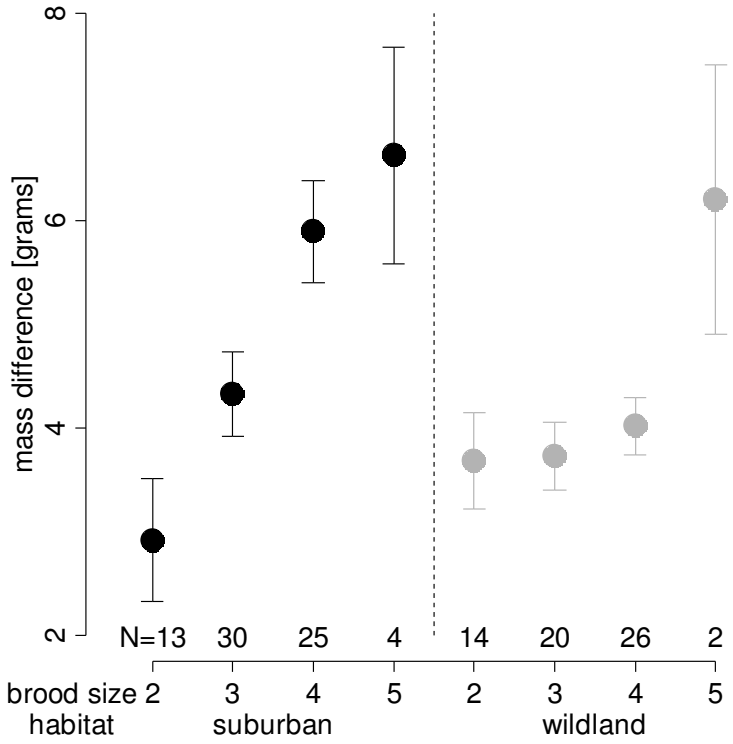

Figure 2: Mass asymmetry (difference between the mass of the heaviest and lightest nestling per brood) ± SE of 3 day old nestlings depending on brood size in the suburban habitat (black circles) and wildland habitat (gray circles). Control and supplemented nests were pooled. N= number of nests

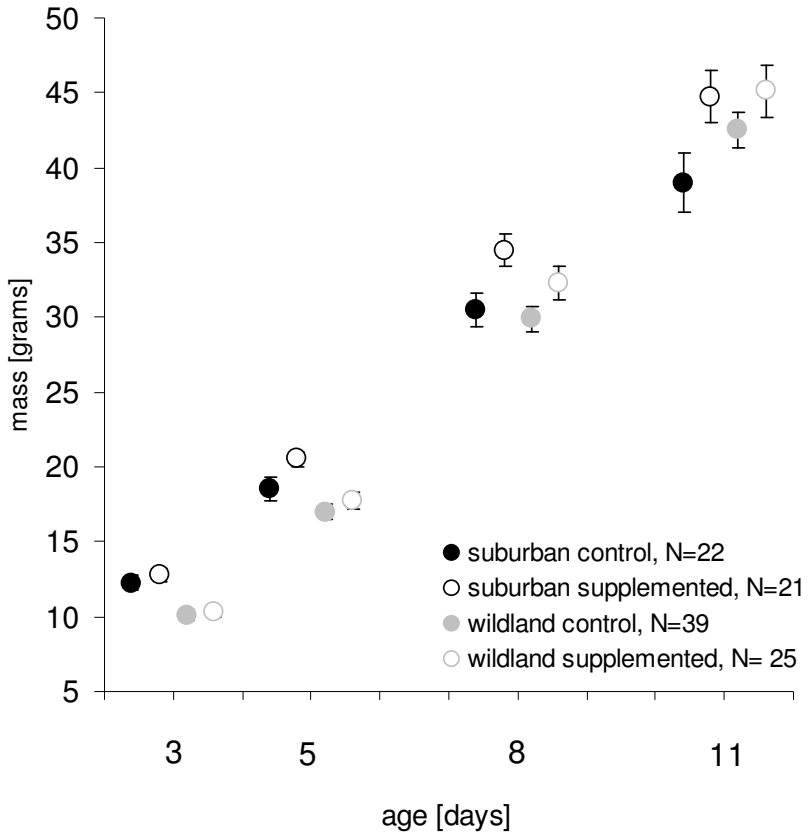

Figure 3: Body mass ± SE at day 3, 5, 8 and 11 post-hatching for nests measured at all ages in relation to habitat and supplementation. Means referring to the same age are separated for clarity.

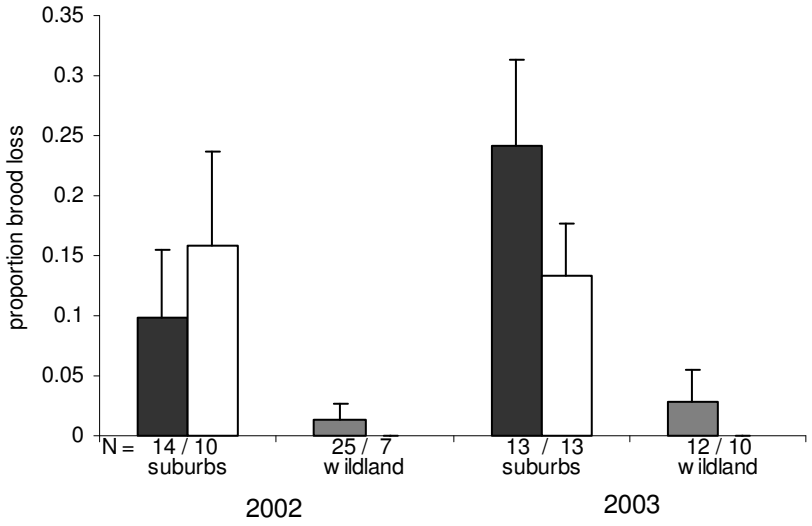

Figure 4: Proportion brood loss (number of nestlings lost/number of nestlings hatched) + SE in relation to habitat, year and supplementation. Filled bars refer to non-supplemented nests, open bars refer to supplemented nests. N= number of nests.

CHAPTER 2

The use of stable isotope analyses to determine the presence of human-provided foods in the diet of nestling Florida scrub-jays

Annette Sauter and Reed Bowman

Abstract

Stable isotope analysis of a consumer's tissue increasingly is used to determine diet composition in wild animals. Human-provided foods are becoming an important resource for many wild animals because as human settlements expand an increasing number of species is exposed to these foods. However, studies on the diet composition within species across a gradient of human settlement and the subsequent potential consequences on fitness are lacking. The goals of this study were to calculate the contribution of human-provided foods to the diet of nestling Florida scrub-jays (*Aphelcoma coerulescens*) in suburban and wildland habitats using stable isotope analyses and to study the impact of these foods on nestling growth. We found that the analysis of stable isotopes is a useful tool to study diet composition in nestling birds, because a diet change in experimentally provisioned nestlings could be detected. However, isotope ratios of $\delta^{15}N$ in plant-based foods, which in the diet of suburban scrub-jays are almost all human-provided, were higher than expected from their trophic position. This resulted in an overlap of $\delta^{15}N$ isotope ratios of plant-based foods and arthropods, the primary food fed to nestlings in wildlands. This overlap prevented the calculation of the precise contribution of plant-based foods to the nestling diet. Nevertheless, we found that suburban nestlings have a high probability of ingesting plant-based foods. The overlap also might explain why we did not find a relationship between the contribution of plant based foods to nestling diet and nestling masses. In addition, the $\delta^{15}N$ and $\delta^{13}C$ ratios of arthropods sampled at a suburban and a wildland site situated 8 km apart, differed by approximately 2 ‰. This difference is of the same magnitude as the difference between two trophic levels, suggesting that food references can vary considerably on a small geographic scale because of anthropogenic influences.

Introduction

Stable isotope analyses of foods and consumers of these foods are increasingly used to understand the composition of the diet of free-living animals (Forero et. al. 2004). Stable isotope mixing models calculate the contribution of the different food sources to the consumers' diet based on the isotope ratios of the food sources and the consumer tissue and correction factors for diet-tissue discrimination. The diet-tissue discrimination (previously "fractionation") factor describes how isotope signatures change between a consumer diet and a specific tissue of interest and is expressed as $\Delta_{dt,}$ which is the isotope ratio of the tissue minus the isotope ratio of diet (Hobson and Bairlein 2003). The diet discrimination factor can be influenced by the physiological characteristics of a species, the nutritional status of an individual, and the composition of the food it consumes (Hobson et al. 1993, Bearhop et al. 2002). Stable isotope mixing models are based on the premise that the ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{13}N$) isotopes in animal tissue reflect those of their diet (DeNiro and Epstein 1981). Changes in the ratios of these isotopes occur via metabolism, protein synthesis and deamination, which cause the 'lighter' isotope to be preferentially lost, and the 'heavier' isotope to be retained. The stable isotope ratios of a consumer are indicative of and heavier than that of their prey; ^{13}C of a consumer is enriched relative to the diet by about 1 ‰, ^{15}N by about 3 ‰ (DeNiro and Epstein 1978, DeNiro and Epstein 1981). Therefore, within a food web animals generally have higher carbon and nitrogen isotope ratios than plants.

Stable isotope analyses have advantages over traditional methods for determining diet composition such as foraging observations, or analysis of gut contents or feces (Pearson et al. 2003). First, the diet composition is measured over a broad period of time. The isotope ratios of a specific tissue reflect the diet composition over the time frame this tissue is synthesized, e.g. a few weeks in feathers (Tieszen et al. 1983) or only a few days in blood plasma (Hobson and Clark 1992). Second, the method is non-destructive because analyses are conducted on easily collected tissues such as hair, feathers or blood (Hobson and Clark 1993). Nevertheless, stable isotope analyses can only be used in dietary studies to discriminate among food sources that differ in isotope ratios. Early mixing models restricted the number of food sources that could be considered, i.e. they only could calculate the contribution of one more food source than the number of isotope groups (e.g. C, N, H) measured, and the food sources could not differ in their elemental concentration

and digestibility. Recent models have eliminated these restrictions (Phillips and Koch 2002, Phillips and Gregg 2003) allowing the method to be more broadly applicable. Given the promising use of stable isotope analyses and the increasing application of this method in a variety of taxa, it is surprising so few stable isotope studies examine the relative importance of human-provided foods in the diet of wild animals (but see Haramis et al. 2001).

Many urban species are thought to profit from the consumption of human-provided foods (Fedriani et al. 2001, Marzluff 2001, Contesse et al. 2004); however, the contribution of human-provided foods in diets and the impacts on fitness of consuming human-provided food often is not known. In Western gulls (*Larus occidentalis*), individuals that depend more on human refuse have lower fitness than individuals that depend more on fish (Annett and Pierrotti 1999). Therefore, further studies on the frequency and impacts of human-provided foods in the diets of animal are needed.

The goal of this study was to compare the diet of nestling Florida scrub-jays that occur in suburban and wildland habitats and to explore whether human-provided foods in the nestling diet are associated with reduced nestling growth in the suburban habitat. Previous studies suggested that the consumption of plant-based human-provided foods negatively affected suburban nestling growth and survival (Shawkey et al. 2004); however, few accurate measures of the diversity of foods in the nestling diet have been made that may help explain sources of variation in nestling growth. Decreased nestling survival contributes to the decline observed in most suburban populations of this species. The Florida scrub-jay is federally listed as Threatened (USFWS 2004) and over 30% of all populations occur within a suburban matrix (Breininger 1999).

The isotope ratios used in our stable isotope mixing model were measured in food reference samples and blood plasma taken from nestlings in both a suburban and wildland site. Before implementing the isotope mixing model we tested the following three assumptions: 1) A change in the diet will be reflected by a change in the plasma isotope ratios of wild nestlings, 2) Isotope ratios of arthropod samples will differ between the suburbs and the wildlands necessitating mixing models with habitat-specific food sources, and 3) Isotope ratios of all food references used in the mixing models will differ from one another.

We used a mixing model for the following analyses: 4) The digestibility of plants by nestling birds was unknown and had to be estimated. We assumed different values for plant

digestibility to assess the effect of variation in plant digestibility on the contribution of the different food sources to nestling diet as calculated by the mixing model. 5) We calculated diet composition for suburban and wildland populations to assess if the contribution of the different food types coincided with previous observational studies and to determine the importance of plant-based foods for the suburban population. 6) Finally we calculated the mean contribution of C3 and C4 plants for each suburban brood separately and entered these contributions into models predicting suburban nestling masses to determine if nestling growth is influenced by diet quality.

Methods

Sample collection and isotope measurements

Study species: Florida scrub-jays are cooperative breeding birds (Woolfenden and Fitzpatrick 1984, 1996). Groups consist of a monogamous breeding pair and up to six non-breeding helpers that defend year-round all-purpose territories. All group members provide food to nestlings and fledglings. Florida scrub-jay adults are omnivorous. In the wildland, the diet varies seasonally and consists of arthropods, small vertebrates and, from late summer through the winter, acorns. In the suburbs, the diet of jays may be similar, but they have year round access to human-provided foods, mainly peanuts and birdseed.

Study populations: We collected nestling blood and food reference samples from suburban and wildland Florida scrub-jay populations of Highlands County, Florida (Bowman and Woolfenden 2001, 2002, Mumme 1992, Schoech et al. 1996). The suburban population is situated at Placid Lakes Estates (27° 10'N, 81°24'W), a residential housing subdivision near Lake Placid. Here, the native scrub vegetation occurs as patches within a matrix of roads and human housing. The wildland study population occurs at Archbold Biological Station, about 8 to 12 km south of the suburban population. In this natural preserve the scrub vegetation is part of a heterogeneous landscape of native and periodically burned habitats, including xeric oak scrub, scrubby flatwoods, rosemary balds and seasonal ponds (Abrahamson et al. 1984). All birds of each population are individually color marked and the sex, social status (breeder, non-breeder), and nest status (building, incubating, brooding) of each jay are known from ongoing long-term studies on the demography of the two populations.

Blood samples*:* We collected all samples between March and June 2003 and 2004. We took blood samples from 11-day-old nestlings via venipuncture of the brachial vein. Blood was collected in 70 µl capillary tubes (Fisherbrand, Fisher Scientific, Pittsburgh, PA). Capillary tubes were kept on ice until return to the laboratory (within 1- 3 h), then they were centrifuged, and the plasma removed and frozen (-20° C). Plasma has a relatively rapid rate of isotopic turnover. Hobson and Clark (1992) found a half-life of approximately 2.9 days in American crows (*Corvus brachyrhynchos*). Thus at day-11, it should reflect the recent diet of nestlings and any maternal contribution to the isotope ratios should be minimized. Each nestling was weighed to the nearest 0.1 g with a 100 g Pesola spring balance.

Food samples*:* We collected arthropods from 18 suburban territories and 17 wildland territories in 2004 when nestlings of these territories were between 5 and 12 days old. In each territory, we used sweep nets through the vegetation. In addition, we searched the same vegetation for 30 minutes to collect lepidopteran larvae; an important food to nestlings scrub-jays that was not well represented in the sweep-net samples. We sorted the two main foods in the nestling diet, lepidopteran larvae and orthopterans (Stallcup and Woolfenden 1978), into morphospecies (suburbs, 2 and 7 morphospecies; wildlands, 13 and 6 morphospecies, respectively). We identified all other arthropods to orders (suburbs, N = 10; wildlands, N = 10). Vertebrate samples were one sandskink (*Neoseps reynoldi*) and one oak toad (*Bufo quercicus*) found dead in the suburbs, and tissue from seven scrub lizards (*Sceloperus woodi*) collected in the wildlands. Plant foods were gathered from local bird feeders and bought in local stores. Bird seeds were the C4 plants corn (*Zea mais,* N = 5), milo (*Sorghum spp.,* N = 8), and millet (*Panicum milleaceum,* N = 10) and the C3 plants peanuts (*Arachis hypogaea,* N = 12*)*, sunflower seeds (*Helianthus annuus,* N = 11) and wheat (including bread, *Triticum aestivum,* N = 12). Waxworms (*Galeria melonella*) samples were taken from three different deliveries from Grubco Inc., Hamilton, OH, because some of the jay groups were experimentally provided with waxworms (see below). We processed samples from each feeder and purchased package separately. All samples were kept frozen (-20° C) until analysis.

Stable isotope analyses: Prior to isotope analyses, we freeze-dried and ground all samples. We removed lipids from the food samples using a Soxhlet apparatus with petroleum-ether as solvent for at least 10 hours. Lipids could not be removed from the

plasma samples because of their small volume. We loaded 1 mg (dry weight) of the plasma or the food samples into tin cups for isotope analyses. Stable isotope ratios were measured on a continuous flow isotope ratio mass spectrometer at the University of Central Florida. Stable isotope ratios are expressed as δ values: $[(R_{sample}/R_{standard})-1] \times 1000$, where δ is the isotope ratio from the sample relative to a standard (Pearson et al. 2003). For C, the international standard is Beedee Belemnite (PDM) limestone formation. For N, the standard is atmospheric N (AIR). R_{sample} and $R_{standard}$ are the fractions of heavy to light isotopes in the sample and standard respectively. Measurement precision was < 0.15 ‰ for N and < 0.10 ‰ for C.

Assumption 1: Detection of diet change using plasma of nestlings

Between March and May 2003, we provided supplemental food to randomly selected jay groups in the suburban and the wildland population and compared isotope ratios in blood plasma between treatment (suburbs: 19, wildland: 13) and control nests (suburbs: 14, wildland: 10). Each day, between day 1 and 10 post-hatching, non-supplemented groups received one peanut broken into pieces and supplemented groups received 30 grams of waxworms (*Galleria mellonella*) on a feeder placed between 10 and 20 meters from the nest. Waxworms are lepidopteran larvae and as such similar to the natural diet of the Florida scrub-jay nestlings (Stallcup and Woolfenden 1978). Jays retrieved waxworms readily from the feeders and carried them to the nest. Nestlings were weighed and bled when eleven days old (for details see above).

We tested whether the isotope ratios in plasma differed between control and supplemented broods using general linear models (proc glm, SAS, SAS Institute Inc. 2001). The dependent variable was the mean $\delta^{13}C$ or $\delta^{15}N$ value per brood in 2003. Habitat, supplementation and habitat x supplementation were the independent categorical variables. For all general linear models run, model fit was assessed using residual plots.

Assumption 2: Differences in isotope ratios of arthropods between habitats

To determine whether we had to calculate diet composition using isotope ratios derived from habitat-specific food sources, we tested for habitat differences in isotope ratios of arthropods. We compared the mean $\delta^{13}C$ and $\delta^{15}N$ of taxonomic groups of arthropods between the habitats using a Wilcoxon signed-rank test. Taxonomic groups

included were Arachnidae, Cicada, Coleoptera, Coleoptera larvae, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera larvae and other arthropods pooled.

Assumption 3: Differences in isotope ratios of food sources within habitats

Before implementing the mixing model we determined whether the food sources differed in isotope ratios. We categorized all individual food samples into the food sources vertebrates, arthropods, C3 and C4 plants. The isotope signatures of $\delta^{13}C$ and $\delta^{15}N$ varied more in arthropods than in vertebrates, C3, or C4 plants (Figure 1). Consequently, using the mean of this food source would have poorly represented the actual arthropod contribution. To get a more accurate estimate, we split the arthropod samples into distinct groups with similar values of $\delta^{13}C$ and $\delta^{15}N$. We used cluster analysis to define clusters of arthropods similar in isotope ratios (proc fastclus, SAS, SAS Institute 2001). We ran the analysis on all arthropod samples measured separately for each habitat. The cluster analysis was repeated, first without then with the waxworm supplement values. All waxworm samples (food supplement) fell into the same cluster, the waxworm source was the mean of all samples in this cluster (3 waxworm samples and 1 to 3 arthropod samples). This gave five distinct clusters of arthropods. Adding in the remaining food sources (vertebrates, C3 and C4 plants), the procedure resulted in 8 food sources for the suburbs and 6 food sources for the wildlands (see Table 1). We did not consider C3 and C4 plants as food sources in the wildland habitat, because wildland nestlings receive animal foods exclusively (Stallcup and Woolfenden 1978). Then, we corrected the isotope ratios for diet-tissue discrimination. Few diet-plasma discrimination factors have been derived for birds, thus we relied on two studies on the yellow-rumped warbler (*Dendroica coronata*, Pearson et al. 2003, Podlesak 2005), because they specified $\delta^{13}C$ and $\delta^{15}N$ diet-plasma diet-tissue discrimination factors for C3 and C4 plants and animal foods. For both arthropod and vertebrate $\delta^{13}C$ diet-plasma discrimination we used two values, 0.6 (positive Δ_{dt}) taken from Pearson (2003) and –1.5 (negative Δ_{dt}), which we visually derived from our own data as done by Newsome et al. (2004). We used two values, because the application of positive Δ_{dt} resulted in some of the plasma signatures laying outside of the mixing polygon (Figure 1c). Signatures outside of the mixing polygon indicate that either an important food source is missing or the discrimination factor assumed is not correct. To ensure that all plasma signatures were within the mixing polygon we visually derived the negative $\delta^{13}C$ animal-plasma

discrimination factor (Δ_{dt}). For this, we used only samples from the wildland because wildland nestlings feed exclusively on animal matter. We calculated the mixing model twice, with the same isotope signatures of food sources and consumer tissue but with either positive Δ_{dt} or negative Δ_{dt} for both arthropod and vertebrate sources unless stated otherwise. For $\delta^{13}C$ C4-plasma discrimination we used –2.6 (Podlesak et al. 2005). For $\delta^{13}C$ C3-plasma fractionation, Pearson et al. (2003) found a value of –1.5 (-1.7, -1.4, 95% C.I.), but Podlesak et al. (2005) report a value of 0.1 ± 0.2. We used -1.5 $\delta^{13}C$ as C3-plasma discrimination factor to ensure that the isotope ratios lay within the mixing polygon of the suburban signatures as done above. Because the discrimination factor for C3 plants lay within the range of values reported in the literature, we employed only this factor. For $\delta^{15}N$ we always used the same diet-tissue discrimination: 2.5 for C3 and C4, and 3.0 for arthropods and vertebrates (Pearson et al. 2003). Finally, we ran general linear models (proc glm, SAS, SAS Institute Inc. 2001) with $\delta^{13}C$ or $\delta^{15}N$ ratios of all food samples as dependent variable and the food source as categorical independent variable. We tested all combinations of isotope signatures after correction for diet discrimination that we subsequently used in the mixing model.

Isotope mixing model

We calculated the range of the contribution of vertebrates, arthropods, C3 plants and C4 plants to the diet of nestlings with the concentration-dependent mixing model for multiple sources, based on Newsome et al. (2004) who combined the models underlying the software programs IsoConc (Phillips and Koch 2002) and IsoSource (Phillips and Gregg 2003), thus, allowing to calculate the source contribution of multiple sources differing in elemental concentration. The mixing model evaluates all combinations of each food source (from 0-100 %) in user-defined increments (in this case, 2%) to identify source combinations that sum to the known isotope signature of the mixture (in this case, blood plasma), within a prescribed small tolerance (in this case, ± 0.1 %). In addition, the mixing model corrects for differences in C and N elemental concentrations and digestibility of the different food sources. With the solutions of the mixing model we created a distribution of the frequency and range of the potential contribution of the different food sources. The mixing model does not offer a unique solution, but it does allow evaluation of the statistical constraints on the relative contributions of different food sources. The calculations were

based on the following assumptions about food stoichometry (weight %): protein, 52% carbon, 16% nitrogen; lipid, 75% carbon; carbohydrate, 45% carbon (Robbins 1993). The elemental composition of plant fibers (USDA 2005) was not included, because nestling birds likely do not digest them. After the mixing model calculated the contributions of all food sources individually, we summed the arthropod contributions for each feasible combination of food sources because we were interested in the total contribution of the arthropod sources.

Sensitivity of the mixing model to variation in assumed digestibility

To estimate the dependence of the calculated contribution of each food source on the assumed digestibility of that source, we calculated the contribution of food sources with different assumptions of plant protein, lipid and carbohydrate digestibility (85%, 50%, 15% and 5 %). We used the mean isotope signature of the non-supplemented suburban nestlings in 2003 and 2004 as the signature of the consumer tissue and positive Δ_{dt}. Digestibility of animal tissue (both fat and protein) always was assumed to be 85% (Klasing 1998). Table 2 shows the diet composition and digestibility data used in modeling.

Population differences

To compare the relative contribution of the food sources in the different study populations, we calculated the mean of the plasma isotope ratios for each population separated by year and supplementation treatment (N= 6) and entered these means as the isotope signature of the consumer tissue and the isotope signatures of the food sources reported in Table 1 in the mixing model.

Plant contributions to suburban broods and suburban brood masses

To explore the importance of plant-based foods in the diet of suburban nestlings in more detail, we used the mean plasma isotope ratio for each non-supplemented suburban brood as isotope signature of the consumer tissue and the food sources for non-supplemented suburban broods (Table 1) and calculated the mean contribution of C3 and C4 plant to each of the 47 broods with the mixing model. Supplemented broods were excluded because these broods probably received more food in addition to food of different quality. We then tested if brood masses varied with $\delta^{13}C$, $\delta^{15}N$, and the mean contribution

of both C3 and C4 plants in the nestling diet. We ran general linear models (proc glm, SAS, SAS Institute 2001) with brood mass as the dependent variable. Independent variables were either $\delta^{13}C$ and $\delta^{15}N$ values, or the contribution of C3 plants and contribution of C4 plants to the diet of each brood. We included year (2003, 2004), helper presence (no, yes), Julian hatch date and brood size as additional independent variables in both models. The contribution of C3 plants was arc-sine square-root transformed and brood sizes were square-root transformed. Year and helper presence were coded as categorical variables. We tested all two-way interactions and removed the non-significant ones to build the final models.

Results

Assumption 1: Detection of diet change using plasma of nestlings

Both $\delta^{13}C$ ($F_{1, 41}$= 21.65, P< 0.01) and $\delta^{15}N$ ($F_{1, 41}$= 75.21, P< 0.01) increased with food supplementation. In addition, $\delta^{15}N$ values ($F_{1, 41}$= 8.23, P< 0.01) but not $\delta^{13}C$ ($F_{1, 41}$= 0.00, P= 0.98) were higher in the suburbs than the wildlands. The $\delta^{13}C$-habitat interaction ($F_{1,41}$= 0.01, P= 0.92) and $\delta^{15}N$-habitat interaction ($F_{1,41}$= 0.30, P= 0.59) were not significant. The $\delta^{13}C$ ratios were positively correlated with the $\delta^{15}N$ ratios (Pearson correlation coefficient= 0.651, N= 48, P< 0.01).

Assumption 2: Differences in isotope ratios between habitats

The same taxonomic groups of arthropods had on average (± SE) a 1.77 ± 0.58 higher $\delta^{13}C$ ratio and a 1.90 ± 0.57 higher $\delta^{15}N$ ratio in the suburbs than in the wildlands (Wilcoxon signed rank test, N= 10, $\delta^{13}C$: S= 25.5, P= 0.006, $\delta^{15}N$: S= 24.5, P= 0.009). Therefore, food samples could not be pooled across habitats for the mixing model.

Assumption 3: Differences in isotope ratios among food sources within habitats

The $\delta^{13}C$ and $\delta^{15}N$ ratios of the food samples from which we took individual measures of the isotopic ratios (see section food samples above) differed among the eight pre-defined suburban food sources and six pre-defined wildland food sources (vertebrates, five arthropod groups, C3 and C4 plants) independent of the diet discrimination factor applied. The $\delta^{13}C$ ratio among food sources differed for positive Δ_{dt} and negative Δ_{dt} in suburban control broods ($F_{7, 70}$= 47.87, P< 0.01, $F_{7, 70}$= 55.98, P< 0.01, respectively), in

suburban supplemented broods ($F_{7, 73}$= 58.16, P< 0.01, $F_{7, 73}$= 7.43, P< 0.01 respectively), in wildland control broods ($F_{5,30}$= 77.88, P< 0.01, $F_{5,30}$= 96.41, P< 0.01, respectively) and wildland supplemented broods ($F_{5,33}$= 123.57, P< 0.01, $F_{5,33}$= 105.10, P< 0.01, respectively). The $\delta^{15}N$ ratios differed among food sources in suburban control broods ($F_{7,70}$= 8.27, P< 0.01), suburban supplemented broods ($F_{7,73}$= 316.21, P< 0.01), wildland control broods ($F_{5,30}$= 77.88, P< 0.01) and wildland supplemented broods ($F_{5,33}$= 147.87, P< 0.01). Thus, the eight suburban and six wildland food sources used for modeling are isotopically distinct.

Sensitivity of the mixing model to variation in digestibility assumed

The absolute contributions of vertebrates, arthropods, C3 plants, C4 plants and waxworms in the diet of non-supplemented suburban broods depended on the plant digestibility assumed (Table 3). Mean contributions of all foods varied at most by 10%. The relative contribution of vertebrates, arthropods, plants and waxworm supplement did not depend on the plant digestibility assumed. Because of the relatively low sensitivity of the mixing model to variation in digestibility assumed, we used the medium value of 50% plant digestibility for further modeling.

Population differences

The absolute contribution of the different food sources depended on population, year, habitat and $\delta^{13}C$ diet-plasma discrimination (Δ_{dt}) assumed (Table 4a and b). For positive Δ_{dt}, we found that the calculated mean contribution of vertebrates ranged between 0.02 and 0.24 and were lower than the sum of the arthropod contributions independent of the population, supplementation and year. The mean contributions of arthropods varied more than the vertebrate contributions (0.22-0.97) and were lower in the suburban than the wildland population. In the suburbs in 2003, the C3 plant contribution was higher than the vertebrate, arthropod and C4 plant contribution (Figure 2). In 2004, the C3 plant contribution was lower than the arthropod contribution, but higher than the other food sources. The C4 plant contribution always was lower than all other food source contributions. In all mixing models with positive Δ_{dt} calculated for the suburbs, more than 99% of the solutions contained a C3 or C4 plant contribution, i.e. diets excluding plants

were unlikely. The mean contribution of the supplemental waxworms was lower in the suburbs than the wildlands.

The contributions of the food sources found for negative Δ_{dt} (Table 4b) were similar to those found for positive Δ_{dt}. The results of the model with negative Δ_{dt} differed from the model with positive Δ_{dt} in that, in the suburbs the mean vertebrate and arthropod contribution tended to be higher, and the mean C3 plant contribution lower; in the wildlands the vertebrate contribution increased and the arthropod contribution declined. In addition, in supplemented broods the contribution of waxworms decreased in suburban broods, but increased in wildland broods. With negative Δ_{dt} a higher percentage of the solutions had no plant contribution than with positive Δ_{dt}, but the percentage was not higher than 3.5 % in any of the solution distributions calculated by the mixing model.

Plant contributions to suburban broods and suburban brood masses

We tested for potential factors influencing the mean day-11 brood masses measured in non-supplemented suburban broods (N= 47, Table 5, Figure 3). The $\delta^{13}C$ ratio was correlated positively with the $\delta^{15}N$ ratios, negatively with the contribution of C3 plants and positively with the contribution of C4 plants per brood ($\delta^{15}N$: Pearsons correlation coefficient= 0.549, P< 0.001; C3 plants, Pearsons correlation coefficient= -0.838, P< 0.001; C4 plants, Pearsons correlation coefficient= 0.736, P< 0.001). $\delta^{15}N$ ratios correlated negatively with the contribution of C3 plants and positively with the contribution of C4 plants (C3 plants, Pearsons correlation coefficient = -0.434, P= 0.002; C4 plants, Pearsons correlation coefficient= 0.426, P< 0.003). We found no association between day-11 brood masses and $\delta^{13}C$, $\delta^{15}N$, the contribution of C3 and C4 plants, helper presence or hatch date independent of the assumed value of Δ_{dt}. Brood mass was higher in 2003 than in 2004 and decreased with brood size when we assumed a negative Δ_{dt} (Table 5a +b); with positive Δ_{dt} the effect of brood size was not statistically significant (Table 5c + d).

Discussion

Determination of nestling diet using stable isotopes

Our study suggests that stable isotopes are a useful tool to study variation in the diet of wild nestlings because it detected short-term changes in their diet. To our knowledge few studies have attempted to determine nestling diet composition using stable isotopes (Knoff

et al. 2002, Dominguez et al. 2003, Forero et al. 2004). It is important to consider that the plasma isotope ratios of nestlings are not determined exclusively by their diet. Isotope signatures of plasma from nestlings may be influenced by the maternal contribution through the eggs. This effect will decrease with nestling age and in our study this effect was probably small because after 10 days around 90% of the blood plasma should have been replaced.

We also found that isotope signatures of food sources can vary between adjacent suburban and wildland habitats. Our arthropod food sources had different isotope ratios in the suburban and the wildland habitat, even though the two sites were only 8 km apart; thus it is crucial to consider anthropogenic changes in isotopic ratios and to use local food sources when choosing references for the mixing models. Biases in isotope models can be introduced by using isotope signatures for food references from the literature (e.g. Szepanksi et al. 1999), from samples that have not been collected over the entire range of the consumer's habitat or from samples collected outside of a consumers habitat. We detected a difference of approximately 2‰ in $\delta^{13}C$ and $\delta^{15}N$ ratios in arthropods between the suburbs and the wildlands habitats, a large difference considering that $\delta^{13}C$ ratios increase typically by 1‰ and, $\delta^{15}N$ ratios by 3-4‰ from one trophic level to the next (DeNiro and Epstein 1978, DeNiro and Epstein 1981). In our study, the isotope ratios of arthropods may vary because they feed on different vegetation in the different habitats. Fry et al. (1978) found a range in isotope signatures of different grasshopper species similar to the range observed in this study and suggested that the variation resulted from different contributions of C3 and C4 plants in the grasshopper diets. Because the plant community composition differs between suburban and wildland habitats, arthropods in suburban habitats may feed more heavily on C4 plants than arthropods in wildland scrub. Alternatively, the isotope ratios of the same plants may vary between habitats. In the suburban habitat, non-native vegetation often is fertilized which can increase $\delta^{13}C$ and $\delta^{15}N$ ratios (Hogberg 1991, Jenkinson et al. 1995). Because some of the nitrogen used for fertilization also will be transferred to the native vegetation, directly through the air or through runoff, the native vegetation might vary in isotope signatures between the suburbs and the wildland habitat. In addition, irrigation in the suburban habitat could change soil chemistry and therefore, lead to differences in isotope signatures of the soils (Bedard-Haughn et al. 2003).

We found that the $\delta^{15}N$ ratios of plant-based human-provided foods were similar to the $\delta^{15}N$ ratios of arthropods, which supports the concern about being careful in the choice of food references. Plant-based human-provided foods may have higher $\delta^{15}N$ ratios than expected from their trophic level because they were fertilized (Hogberg 1991) or because they were grown on soils outside of the study area (Bedard-Haughn et al. 2003). Because human-provided foods may derive their isotope signatures from vastly different sources than the native foods available to organisms (human-provided foods often are manufactured elsewhere and have a variety of added supplements, such as pet foods and bread) their isotope signatures may not be indicative of their true trophic level. In this study, the overlapping $\delta^{15}N$ ratios of plant-based human-provided foods and arthropods (Figure 1) resulted in an overlapping range of possible contributions of plant and arthropod food sources (Figure 2), thus, preventing a definitive discrimination of the exact contribution of human-provided foods in the diet of nestling scrub-jays in suburban habitats.

Sensitivity of the mixing model to variation in assumed digestibility

The food source contributions that the mixing model calculated were relatively insensitive to variation in the assumed digestibility of plant food sources. The relative contribution of all food sources did not change with variation in assumed plant digestibility and the absolute contributions of all food sources did not vary by more than 10%. Therefore, we believe the mixing model implemented in this study can be applied even if knowledge about digestive ability of a consumer is lacking. However, the sensitivity of the model to variation in digestive abilities should be explored in each case.

Population differences

The diet composition derived from the mean isotope ratios of the suburban and wildland populations support previous studies suggesting that arthropods are the main food provided to nestlings and that vertebrates comprise a minor fraction of the diet (Stallcup and Woolfenden 1978). Nevertheless, we had not expected that the vertebrate contribution would be higher than the arthropod contribution in some calculations and that the contribution of the supplemented waxworms would be higher in the wildland than in the suburban habitat. Wildland nestlings suffer less from food limitation than suburban nestlings (Shawkey et al. 2004) and suburban parents seem to be able to fulfil their own

nutritional needs with human-provided food (Fleischer et al. 2003). We anticipated that suburban parents would bring more of the waxworms to their nestlings than the wildland parents. Both of these unexpected results may be explained by the high variation in isotope signature of the arthropods and the similarity of the isotope signatures of waxworms, vertebrates and some arthropods. This similarity and the resulting high variation in possible contributions of these food sources did not allow a complete separation of the possible contribution of the latter three sources. The high variation suggests that the calculated mean contribution might be a poor estimate of the actual contribution of a given food source. Unfortunately, we lack a more precise measure. The high variation also probably caused us to attribute some of the contribution of arthropods to vertebrates or waxworms, or vice versa. For example in suburban supplemented broods in 2003, we estimated the contribution of waxworms to the diet at 2% and vertebrates at 50%, but waxworms were provided daily in large amounts and birds were observed regularly delivering them to nestlings. In contrast, during observations conducted while parents were provisioning nestlings in 2004, less than 1% of the animal foods encountered while foraging were vertebrates (Sauter et al. unpublished, chapter 4), suggesting that our models vastly overestimated the contributions of vertebrates and underestimated the contribution of waxworms. In addition, the waxworm contribution might be biased because the supplementation not only changed the quality of the diet but it also likely affected the nutritional status of the young which can influence diet-tissue discrimination (Hobson et al. 1993).

Our results support previous observations (Shawkey 2001) that suburban jays feed their nestlings plant-based human-provided foods; more than 97% of all possible combinations of food sources contained some C3 or C4 contribution. C4 plants, e.g. milo, millet and cracked corn, do not seem to be an important food source of suburban nestlings. They contributed at most, 16% of the diet in both years of our study. Shawkey (2001) observed suburban parents feeding millet to nestlings, but nestlings may not be able to assimilate these seeds. C3 plants seem to be more important than C4 plants; however, the exact contribution of C3 plants remains unclear. The calculated contributions of C3 plants to suburban broods varied considerably and depended on the assumed value for $\delta^{13}C$ animal-plasma discrimination (Δ_{dt}). With positive Δ_{dt} the estimated mean contribution of plant based foods was 64%, with negative Δ_{dt} it was 28%. We think that 28% is closer to

the actual value for the following reasons. The diet of female scrub-jays in the suburbs consists of about 30% human-provided foods immediately prior to the breeding season (Fleischer et al. 2003). In experimental trials, suburban parents prefer feeding nestlings arthropods (Sauter et al. submitted, chapter 3), but observations of normal foraging and nestling feeding demonstrates that 15% of the foods taken to the nests were plant-based (Sauter et al. unpublished, chapter 4). Because nestlings may extract fewer nutrients from plant-based foods than adult birds (Karasov and Wright 2002), scrub-jay nestlings probably do not assimilate all of the 15% plant foods they receive. Consequently, an assimilated proportion of 64% C3 plants seems to overestimate the actual C3 plant contribution.

We might have wrongly assumed a positive value for $\delta^{13}C$ animal-plasma Δ_{dt}, because information about diet-tissue discrimination and the factors influencing it is still lacking (Hobson et al. 1993, Bearhop et al. 2002). The positive Δ_{dt} we used had been measured in adult birds that were not nutritionally stressed. The actual Δ_{dt} could be negative because nestlings differ from adults in their physiology or because nestling were nutritionally stressed. In support for negative Δ_{dt} in nestlings, the feather tips of 5 week old laughing gulls (*Larus atricilla*) had slightly lower $\delta^{13}C$ values than the base of the same feathers; i.e. the feather parts grown earlier had more negative values than the feather parts grown later, suggesting differences in diet discrimination with age (Knoff et al. 2002). However, the lower values also could have resulted from variation in diet composition. Starving individuals tend to mobilize endogenous resources and using endogenous instead of exogenous resources influences diet discrimination. Bearhop et al. (2002) found that $\delta^{13}C$ but not $\delta^{15}N$ decreased with mass loss in great skuas (*Catharacata skua*) and Hobson et al. (2004) reported a decrease of $\delta^{13}C$ in fasting female redhead ducks (*Aythya americana*). In contrast, Hobson et al. (1993) reported that $\delta^{15}N$ but not $\delta^{13}C$ decreased with mass loss in American crows (*Corvus brachyrhynchos).* However, we did not detect any relationship between brood masses and the $\delta^{13}C$ or $\delta^{15}N$ ratios of the broods.

Alternatively, Δ_{dt} might not be negative, but the $\delta^{13}C$ ratios of the animals references measured might have been higher than the $\delta^{13}C$ ratios of arthropods assimilated by the nestlings. This might be a consequence of not removing the non-digestible chitin portion from our food references prior to analysis. Schimmelmann and DeNero 1986(1987) found that $\delta^{13}C$ ratios for chitin were higher than $\delta^{13}C$ ratios of the diet in three out of five invertebrate species. We also could have underestimated the $\delta^{13}C$ ratios in assimilated food

because we removed lipids from the arthropod references but not from the plasma samples from which the ratios of assimilated foods were derived. The small volume of plasma obtained from nestlings prevented us from removing lipids. Lipids tend to have lower $\delta^{13}C$ ratios than the entire organic matter (Bearhop et al. 2002 but see Tieszen et al 1983). Although lipid concentrations in blood plasma are low, they increase shortly after a meal, possibly influencing isotope ratios (Bearhop et al. 2002).

Plant contribution and suburban nestling masses

In this study, we found no relationship between brood masses in the suburban habitat and the mean contribution of plant foods to the brood's diet or the isotope signature of the brood. This may be true or our measure of the plant contribution in the nestling diet may be a poor estimate of the actual importance of plant foods in nestling diet. The latter is likely in this study, because the isotope signatures of the food references used did not allow for separation of the contributions of arthropod and C3 plant foods. The lack of separation is indicated by the considerable overlap of the possible contributions of arthropods and C3 plants resulting from the mixing model (Figure 2). The inaccuracy of our measures of the C3 plant contribution also is supported by the strong correlation between the mean contribution of C3 plants and the $\delta^{13}C$ ratios and the $\delta^{15}N$ ratios in the plasma. Hence, a concurrent increase of $\delta^{13}C$ ratios and the $\delta^{15}N$ ratios will lead to a decrease in the calculated mean C3 plant contribution; however, the same increase could result from the nestlings being fed different groups of arthropods without any decrease in the input of plant based foods. In our study the inaccuracy resulted from the plant sources having the same ranges in $\delta^{15}N$ ratios as the arthropod sources, possibly as the result of a variety of artifacts associated with growing in an urban environment. In other urban habitats, this may not be the case, hence, other studies might obtain more precise estimates of the contributions of human-provided foods to diets than found in this study.

In summary, we found that analyses of stable isotopes are a useful tool to study diet composition in nestling birds. However, applicability of the analyses of stable isotopes for the determination of the importance of a human-provided diet in other species will depend strongly on the type and the isotope ratios of human-provided and natural foods available in a food web. Despite the limitations revealed in this study, we think that it is worthwhile evaluating the use of stable isotope analyses to determine the importance of human-

provided foods for other declining urban species as the method is widely applicable, efficient and non-destructive.

Acknowledgements

We thank J. Roth and K. Hobson for assistance in developing the methodology and J. Roth for the use of the stable isotope facilities at the University of Central Florida, Orlando. S. J. Schoech and G. Woolfenden permitted access to their study populations and demographic data. D. Phillips provided us with the SAS code to run the mixing model. K.G. Ashton collected the scrub lizard tissues. This manuscript benefited from the comments of J. Roth, K. Hobson, K. Schiegg and U. Steiner. AS was supported by a graduate research internship at Archbold Biological Station, and by the American Ornithologists' Union, Basler Stiftung für biologische Forschung, DeGiacomi Foundation, Florida Ornithological Society, Janggen-Pöhn Foundation, Roche Research Foundation, and Wolfermann-Nägeli Foundation. Research in the suburban and wildland sites was supported by NSF grants IBN-0077469 and -0346557 to RB, grants IBN-9983201, -0235821, and -0346328 to Stephan J. Schoech. All research on this listed species was permitted by the US Fish and Wildlife Service (permit TE824723-5 to Reed Bowman).

References

Abrahamson, W. G., A. F. Johnson, J. N. Layne, and P. A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. Florida Scientist **47**:209-250.

Annett, C. A., and R. Pierrotti. 1999. Long-term reproductive output in Western Gulls: consequences of alternate tactics in diet choice. Ecology **80**:288-297.

Bearhop, S., S. Waldron, S. C. Votier, and R. W. Furnes. 2002. Factors That Influence Assimilations Rates and Fractionation of Nitrogen and Carbon Stable Isotopes in Avian Blood and Feathers. Physiological and Biochemical Zoology **75**:451-458.

Bedard-Haughn, A., J. W. van Groeningen, and C. van Kessel. 2003. Tracing ^{15}N through landscapes: potential uses and precautions. Journal of Hydrology **272**:175-190.

Bell, G. P. 1990. Birds and mammals on an insect diet: a primer on diet composition analysis in relation to ecological energetics. Studies in Avian Biology **13**:416-422.

Bowman, R., and G. E. Woolfenden. 2001. Nest success and the timing of nest failure of Florida Scrub-Jays in suburban and wildland habitats. Pages 383-402 *in* J. M. Marzluff, R. Bowman, and R. E. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, New York.

Bowman, R., and G. E. Woolfenden. 2002. Nest site selection by Florida Scrub-Jays in natural and human-modified habitats. Wilson Bulletin **114**:128-135.

Breininger, D. R. 1999. Florida Scrub-Jay Demography and Dispersal in a Fragmented Landscape. Auk **116**:520-527.

Contesse, P., D. Hegglin, S. Gloor, F. Bontadina, and P. Deplazes. 2004. The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. Mammalian Biology **69**:81-95.

Cosgrove, J. J., D. H. Beermann, W. A. House, B. Toddes, and E. S. Dierenfeld. 2002. Whole-Body Nutrient Composition of Various Ages of Captive-Bred Bearded Dragons (*Pogona vitteceps*) and Adult Wild Anoles (*Anolis carolensis*). Zoo Biology **21**:489-497.

Crissey, S. D., B. Toddes, and K. A. Slifka. 1999. Micronesian Kingfishers: Nutrition and dietary husbandry. Nutrition advisory group handbook:Fact Sheet 009.

DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimimica et Cosmochimica Acta **42**:495-506.

DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta **45**:341-351.

Dominguez, L., W. A. Montevecchi, N. M. Burgess, J. Brazil, and K. A. Hobson. 2003. Reproductive success, environmental contaminants, and trophic status of nesting Bald Eagles in eastern Newfoundland, Canada. Journal of Raptor Research **37**:209-218.

Fedriani, J. M., T. K. Fuller, and R. M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography **24**:325-331.

Fleischer, A. L., R. Bowman, and G. E. Woolfenden. 2003. Variation in foraging behavior, diet and the time of breeding of Florida Scrub-Jays in suburban and wildland habitats. Condor **105**:515-527.

Forero, M. G., G. R. Bortolotti, K. A. Hobson, J. A. Donazar, M. Bertelloti, and G. Blanco. 2004. High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. Journal of Animal Ecology **73**:789-801

Fry, B., A. Joern, and P. L. Parker. 1978. Grasshopper food web analysis: us of carbon isotope ratios to examine feeding relationships among terrestrial herbivores. Ecology **59**:498-506.

Grubco. 2005. Nutritional information, http://www.grubco.com/Nutritional_Information.cfm.

Haramis, G. M., D. G. Jorde, S. A. Macko, and J. L. Walker. 2001. Stable-isotope analysis of canvasback winter diet in upper Chesapeake bay. Auk **118**:1008-1017.

Hobson, K. A., R. T. Alisauskas, and R. G. Glark. 1993. Stable-nitrogen enrichment in avian tissues due to fasting and nutritional stress: Implications for isotopic analysis of diet. Condor **95**:388-394.

Hobson, K. A., L. Atwell, L. I. Wassenaars, and T. Yerkes. 2004. Estimating endogenous nutrient allocations to reproduction in Redhead Ducks: a dual isotope approach using dD and d13C measurements of female and egg tissues. Functional Ecology **18**:737-745.

Hobson, K. A., and F. Bairlein. 2003. Isotopic fractionation and turnover in captive Garden Warblers (*Sylvia borin*): implications for delineating dietary and migratory associations in wild passerines. Canadian Journal of Zoology **81**:1630-1635.

Hobson, K. A., and R. G. Clark. 1992. Assessing avian diets using stable isotopes I: Turnover of ^{13}C tissues. Condor **94**:181-188.

Hobson, K. A., and R. G. Clark. 1993. Turnover of ^{13}C and Plasma Fractions of Blood: Implications for Nondestructive Sampling in Avian Dietary Studies. Auk **110**:638-641.

Hogberg, P. 1991. Development of N-15 Enrichment in a Nitrogen-Fertilized Forest Soil Plant-System. Soil Biology & Biochemistry **23**:335-338.

Jenkinson, D. S., K. Coleman, and D. D. Harkness. 1995. The Influence of Fertilizer Nitrogen and Season on the C-13 Abundance of Wheat-Straw. Plant and Soil **171**:365-367.

Karasov, W. H., and J. Wright. 2002. Nestling digestive physiology and begging. Pages 199-219 *in* J. Wright and M. L. Leonard, editors. The evolution of begging: competition, cooperation and communication. Kluwer Academic Publishers, Dordrecht, Netherlands.

Klasing, K. G. 1998. Comparative avian nutrition. CAB International, Oxon, UK.

Knoff, A. J., S. A. Macko, R. M. Erwin, and K. M. Brown. 2002. Stable isotope analysis of temporal variation in the diets of pre-fledged Laughing gulls. Waterbirds **25**:142-148.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19-48 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwall, MA.

Moreby, S. J., and C. Stoate. 2000. A quantitative comparison of neck-collar and faecal analysis to determine passerine nestling diet. Bird Study **47**:320-331.

Mumme, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. Behavioral Ecology and Sociobiology **31**:319-328.

Newsome, S. D., D. L. Phillips, B. J. Culleton, T. P. Guilderson, and P. L. Koch. 2004. Dietary reconstruction of an early to middle Holocene human population from the central California coast: insights from advanced stable isotope mixing models. Journal of Archaeological Science **31**:1101-1105.

Pearson, S. F., J. L. Douglas, C. H. Greenberg, and C. Martínez del Rio. 2003. Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. Oecologia **135**:516-523.

Phillips, D. L., and J. W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia **136**:261-269.

Phillips, D. L., and P. L. Koch. 2002. Incorporating concentration dependence in stable isotope mixing models. Oecologia **130**:114-125.

Podlesak, D. W., S. R. McWilliams, and K. A. Hatch. 2005. Stable isotopes in breath, blood, feces and feathers can indicate intra-individual changes in the diet of migratory songbirds. Oecologia **142**:501-510.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Academic Press, Orlando.

Schimmelmann, A., and M. J. DeNero. 1986(1987). Stable isotopic studies on chitin. 2. The $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in arthropod chitin. Contributions in Marine Science **29**:113-130.

Sauter, A., R. Bowman, S. J. Schoech, and G. Pasinelli. submitted. Human-provided foods in suburban habitats: Why do parent Florida scrub-jays (*Aphelocoma coerulescens*) feed them to nestlings? Behavioral Ecology and Sociobiology.

Schoech, S. J., R. L. Mumme, and J. C. Wingfield. 1996. Delayed breeding in the cooperatively breeding Florida scrub-jay (*Aphelocoema coerulescens*): inhibition or the absence of stimulation? Behavioral Ecology and Sociobiology **39**:77-90.

Shawkey, M. D. 2001. Proximate causes of brood reduction in Florida Scrub-Jays. M.Sc. thesis. University of South Florida, Tampa.

Shawkey, M. D., R. Bowman, and G. E. Woolfenden. 2004. Why is brood reduction in Florida scrub-jays higher in suburban than in wildland habitats? Canadian Journal of Zoology **82**:1427-1435.

Stallcup, J. A., and G. E. Woolfenden. 1978. Family status and contributions to breeding by Florida Scrub Jays. Animal Behaviour **26**:1144-1156.

Szepanksi, M. M., M. Ben-David, and V. Van Ballenberghe. 1999. Assessment of anadromous salmon resources in the diet of the Alexander Archiepelago wolf using stable isotope analysis. Oecologia **120**:327-335.

Tieszen, L. L., T. W. Boutton, K. G. Tesdahl, and N. A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for d13C analysis of diet. Oecologia **57**:32-37.

USDA. 2005. USDA Nutrient Database. *in*. U.S. Department of Agriculture, http:/www.nal.usda.gov/fnic/foodcomp/.

Woolfenden, G. E., and J. W. Fitzpatrick. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird. Princeton University Press, Princeton, New Jersey.

Woolfenden, G. E., and J. W. Fitzpatrick. 1996. Florida Scrub-Jay *(Aphelocoma coerulescens)*. Pages 1-28 *in* A. Poole, editor. The Birds of North America. American Ornithologists' Union and The Academy of Natural Sciences, Philadelphia.

U. S. Fish and Wildlife Servcie. 2004. Draft revised recovery plan for the Florida scrub-jay. U. S. Fish and Wildlife Service, Atlanta, GA.

Table 1: Isotope data used in modeling. $\delta^{13}C$ for arthropods and vertebrates shown are for positive animal-plasma Δ_{dt} ($\delta^{13}C$ for negative Δ_{dt} are 2.1 lower, for further explanations see methods).

	Control					Supplemented				
Suburban										
Food source	N	$\delta^{15}N$	± SE	$\delta^{13}C$	± SE	N	$\delta^{15}N$	± SE	$\delta^{13}C$	± SE
Arthropod 1[1)]	7	1.63	± 0.26	-22.97	± 0.16					
Arthropod 2[1)]	2	4.35	± 1.72	-17.92	± 0.47					
Arthropod 3[1)]	3	4.01	± 0.77	-11.75	± 0.45					
Arthropod 4	3	5.01	± 0.81	-21.95	± 0.58	4	5.81	± 0.98	-21.91	± 0.41
Arthropod 5	4	8.58	± 0.66	-20.26	± 0.65					
Waxworm						6	9.25	± 0.49	-19.60	± 0.31
Vertebrate[1)]	2	6.89	± 0.00	-20.60	± 0.16					
C3 plant[1)]	34	5.06	± 0.32	-25.62	± 0.42					
C4 plant[1)]	23	5.08	± 0.22	-14.79	± 0.62					
Nestlings 2003	19	4.81	± 0.23	-23.47	± 0.48	14	6.19	± 0.19	-21.83	± 0.39
Nestlings 2004	30	5.24	± 0.18	-21.19	± 0.28					
Wildland										
Food source	N	$\delta^{15}N$	± SE δ	$\delta^{13}C$	± SE	N	$\delta^{15}N$	± SE	$\delta^{13}C$	± SE
Arthropod 1[1)]	17	0.49	± 0.16	-23.86	± 0.85					
Arthropod 2[1)]	2	2.82	± 0.03	-12.46	± 0.78					
Arthropod 3[1)]	6	2.73	± 0.46	-22.64	± 0.66					
Arthropod 4[1)]	3	6.02	± 0.10	-23.77	± 1.32					
Arthropod 5	1	8.45		-20.25						
Waxworm						4	9.45	± 0.41	-19.66	± 0.83
Vertebrate [1)]	7	5.95	± 0.29	-20.29	± 0.84					
Nestlings 2003	13	4.18	± 0.14	-23.49	± 0.33	10	5.87	± 0.20	-21.59	± 0.44
Nestlings 2004	74	4.19	± 0.10	-23.51	± 0.15					

[1)] References used for control and supplemented broods. In the supplemented treatment arthropod 5 was pooled with the waxworm source.

Table 2: Diet composition and digestibility data used in modeling.

Diet	Source	Digesti-bility	Protein N	Protein C	Lipid C	Carbon C	Digestible [N]	Digestible [C]	Digestible C/N
C3 plants[1)]	Peanuts	85 %	3.9	12.6	37.1	3.6	3.3	45.3	13.7
	Sunflower seed	50 %					1.9	26.6	13.7
		15 %					0.6	8.0	13.7
		5 %					0.2	2.7	13.7
C4 plants[1)]	Corn	85 %	1.7	5.5	3.1	29.7	1.4	32.5	22.8
	Sorghum	50 %					0.8	19.1	22.8
	Millet	15 %					0.3	5.7	22.8
		5 %					0.1	1.9	22.8
Arthropod[2)]		85 %	9.6	31.2	11.6	0.0	8.2	36.4	4.5
Vertebrate[3)]	Anolis lizards, Green anole	85%	10.8	35.1	6.8	0.0	9.2	35.6	3.9
Waxworm[4)]		85 %	2.5	8.1	16.6	0.0	2.1	21.0	10.0

Food composition from [1)] USDA 2005 [2)] Bell 1990, [3)] Crissey et al. 1999, Cosgrove et al. 2002 and, [4)] Grubco 2005. Units: g X/100 g dry matter for first four variables; g X/100 for last three. USDA NDB#: peanut 16087, sunflower seeds 12036, corn 20014, sorghum 20067, millet 20031

Table 3: Biomass contribution of food sources to suburban isotopic ratios (non-supplemented nestlings) with different assumptions of plant digestibility (85%, 50% and 15%). Each distribution is defined by the means, 1st and 99th percentile values, which cover 98% of all possible solutions.

				Vertebrate			**Arthropods**			**C3 plant**			**C4 plant**		
Plant digesti-bility	Habitat	Year	# solutions	1%	**Mean**	99%	1%	**Mean**	99%	1%	**Mean**	99%	1%	**Mean**	99%
85 %	Suburban	2003	24078	0.00	**0.06**	0.24	0.14	**0.37**	0.60	0.36	**0.55**	0.78	0.00	**0.01**	0.06
50 %			5928	0.00	**0.05**	0.20	0.10	**0.29**	0.50	0.48	**0.64**	0.84	0.00	**0.01**	0.06
15%			32031	0.00	**0.06**	0.24	0.14	**0.35**	0.58	0.40	**0.55**	0.74	0.00	**0.04**	0.16
5 %			5	0.00	**0.02**	0.02	0.00	**0.06**	0.08	0.90	**0.91**	0.92	0.00	**0.02**	0.04
85 %	Suburban	2004	395668	0.00	**0.14**	0.46	0.22	**0.59**	0.94	0.00	**0.24**	0.58	0.00	**0.03**	0.12
50 %			359428	0.00	**0.14**	0.48	0.22	**0.59**	0.96	0.00	**0.23**	0.60	0.00	**0.02**	0.10
15 %			712339	0.00	**0.15**	0.46	0.24	**0.59**	0.94	0.00	**0.20**	0.46	0.00	**0.06**	0.26
5 %			472495	0.00	**0.15**	0.50	0.24	**0.62**	0.94	0.00	**0.15**	0.56	0.00	**0.07**	0.26

Table 4: Results of the isotope mixing model for positive animal-plasma Δ_{dt} (a) and negative animal-plasma Δ_{dt} (b). Ranges and means of biomass contributions of vertebrates, arthropods, plants and waxworms calculated for mean isotopic ratios per population depending on year and supplementation. Each distribution is defined by the means, 1st and 99th percentile values, which cover 98% of all possible solutions.

a)

Habitat	Year	Supple-mented	# solu-tions	Vertebrate			Arthropods			C3 plants			C4 plants			Waxworm		
				1%	**Mean**	99%	1%	**Mean**	99%	1%	**Mean**	99%	1%	**Mean**	99%	1%	**Mean**	99%
Suburban	2003	no	5928 [1)]	0.00	**0.05**	0.20	0.10	**0.29**	0.50	0.48	**0.64**	0.84	0.00	**0.01**	0.06			
		yes	38057 [2)]	0.00	**0.24**	0.54	0.04	**0.22**	0.54	0.14	**0.34**	0.58	0.00	**0.01**	0.08	0.00	**0.17**	0.48
	2004	no	359428 [3)]	0.00	**0.14**	0.48	0.22	**0.59**	0.96	0.00	**0.23**	0.60	0.00	**0.02**	0.10			
Wildland	2003	no	293	0.00	**0.03**	0.10	0.90	**0.97**	1.00									
		yes	1897	0.00	**0.20**	0.52	0.36	**0.50**	0.70							0.00	**0.30**	0.62
	2004	no	554	0.00	**0.03**	0.10	0.90	**0.97**	1.00									

[1)] 0 solution without C3 or C4 plants, [2)] 0 solution without C3 or C4 plants [3)] 796 solutions without C3 or C4 plants (<0.01 %)

b)

Habitat	Year	Supple-mented	# solu-tions	Vertebrates			Arthropods			C3 plants			C4 plants			Waxworm		
				1%	**Mean**	99%	1%	**Mean**	99%	1%	**Mean**	99%	1%	**Mean**	99%	1%	**Mean**	99%
Suburban	2003	no	191946[1)]	0.00	**0.12**	0.42	0.24	**0.63**	0.96	0.00	**0.24**	0.68	0.00	**0.01**	0.10			
		yes	38537[2)]	0.22	**0.50**	0.76	0.06	**0.28**	0.58	0.00	**0.16**	0.54	0.00	**0.03**	0.10	0.00	**0.02**	0.06
	2004	no	898371[3)]	0.00	**0.15**	0.44	0.28	**0.65**	0.96	0.00	**0.14**	0.50	0.00	**0.06**	0.16			
Wildland	2003	no	12305	0.00	**0.18**	0.52	0.48	**0.83**	1.00									
		yes	1327	0.00	**0.35**	0.90	0.04	**0.20**	0.42							0.02	**0.46**	0.76
	2004	no	12434	0.00	**0.18**	0.52	0.48	**0.82**	1.00									

[1)]6434 solution with less than 0.001 contribution of C3 or C4 plants (3.4 % of all solutions) [2)]1068 solution with less than 0.001 contribution of C3 or C4 plants (2.7 % of all solutions) [3)] 16402 solution with less than 0.001 contribution of C3 or C4 plants (1.8 % of all solutions)

Table 5: Results of general linear models of potential factors affecting mean brood mass at day 11 of non-supplemented suburban broods (N= 48 broods), a) and c) with mean $\delta^{13}C$ and $\delta^{15}N$ signatures and b) and d) with the mean contributions of C3 and C4 plants as independent variables for a) and b) positive animal-plasma Δ_{dt} and c) and d) negative animal-plasma Δ_{dt}.

a)

Source	df	Estimate	SE	F	P
Mean $\delta^{13}C$	1	0.503	0.780	0.41	0.524
Mean $\delta^{15}N$	1	1.600	1.415	1.28	0.267
Year (2003, 2004)	1	4.058	2.403	2.85	0.100
Helper presence (no, yes)	1	-0.930	2.449	0.14	0.706
Julian hatch date	1	-0.006	0.055	0.01	0.907
Brood size	1	-4.221	4.338	0.95	0.337

b)

Source	Estimate	SE	F	P
Mean contribution C3 plant	-7.397	12.686	0.34	0.563
Mean contribution C4 plant	-0.662	4.848	0.02	0.892
	4.553	2.289	3.96	0.054
	-3.074	2.402	1.64	0.208
	-0.035	0.056	0.41	0.523
	-6.214	3.866	2.58	0.116

c)

Source	df	Estimate	SE	F	P
Mean $\delta^{13}C$	1	-0.066	0.676	0.01	0.922
Mean $\delta^{15}N$	1	0.645	1.143	0.32	0.576
Year (2003, 2004)	1	2.222	2.031	1.20	0.281
Helper presence (no, yes)	1	-1.198	2.134	0.32	0.578
Julian hatch date	1	0.009	0.049	0.04	0.842
Brood size	1	-7.759	3.566	4.73	0.056

d)

Source	Estimate	SE	F	P
Mean contribution C3 plant	-6.878	5.523	1.55	0.220
Mean contribution C4 plant	-0.423	1.417	0.09	0.767
	4.569	2.236	4.17	0.047
	-3.057	2.327	1.73	0.196
	-0.029	0.051	0.32	0.574
	-6.342	3.754	2.85	0.099

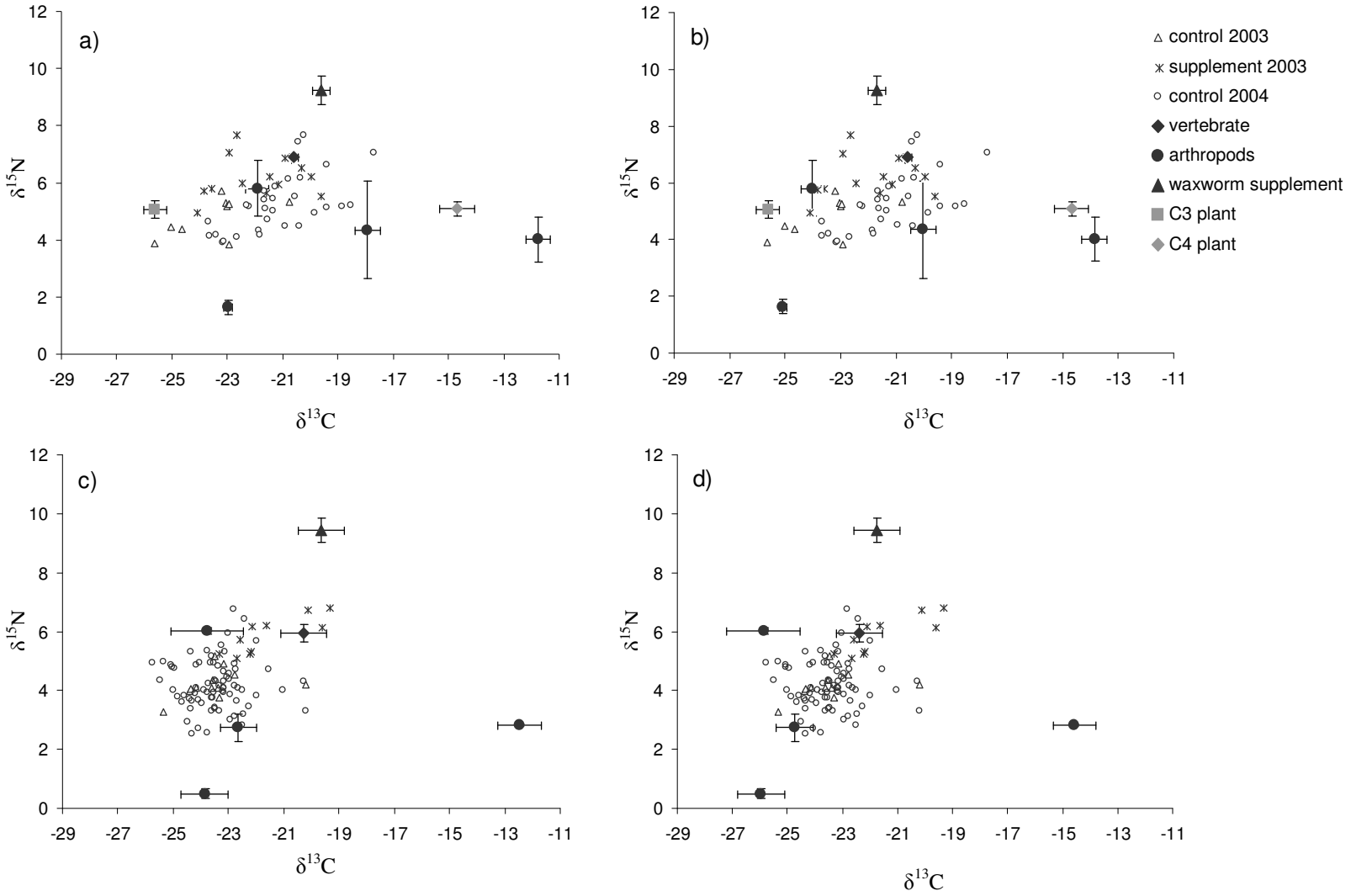

Figure 1: Mean isotopic composition of food sources (± SE, filled symbols) used in modeling and plasma samples (mean per brood, open symbols) for non-supplemented broods in the suburban habitat (a and b) in the wildland habitat (c and d) with positive $\delta^{13}C$ animal-plasma diet discrimination (a and c) and negative $\delta^{13}C$ animal-plasma diet discrimination (b and d). Missing SE are smaller than 0.1

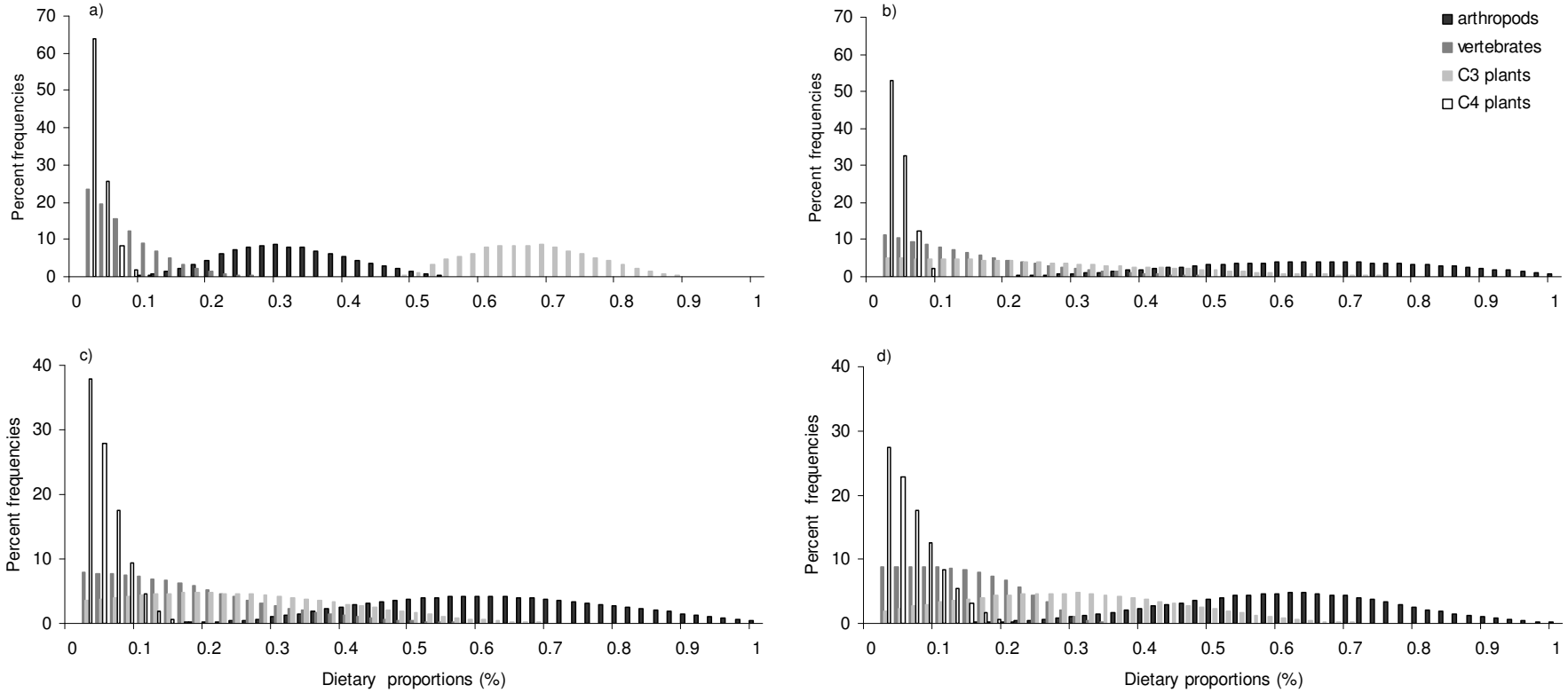

Figure 2: Dietary biomass proportion of the food sources in non-supplemented suburban populations in 2003 (a and b) and 2004 (c and d) positive $\delta^{13}C$ animal-plasma diet discrimination (a and c) negative $\delta^{13}C$ animal-plasma diet discrimination (b and d). The contributions are calculated for all model iterations (in 2 % increments), and are expressed as the percent frequency of all possible solutions. Note scaling differences in y-axes.

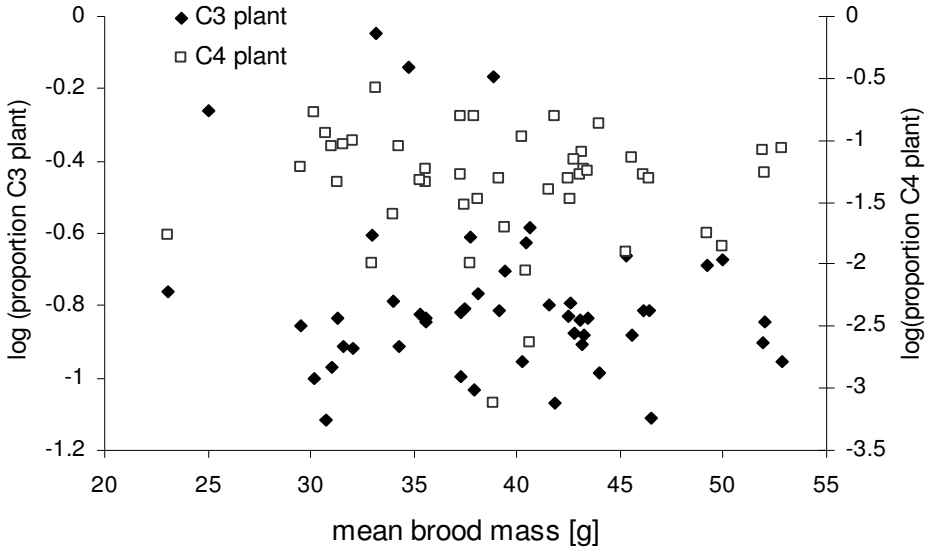

Figure 3: Brood mass in relation to mean biomass contribution of C3 and C4 plants in non supplemented suburban broods (N=47 broods) for negative $\delta^{13}C$ animal-plasma diet discrimination.

CHAPTER 3

Human-provided foods in suburban habitats: Why do parent Florida scrub-jays (*Aphelocoma coerulescens*) feed them to nestlings?

Annette Sauter and Reed Bowman

Abstract

Human-provided foods appear to benefit many adult birds, but can have negative impacts on nestlings. Florida scrub-jays in suburban habitats breed earlier and have clutch sizes larger than wildland jays, but their nestlings have reduced growth and survival, probably because of the inclusion of human-provided foods in nestling diets. We tested experimentally whether parents feed human-provided foods, given the apparent costs, because 1) they do not discriminate between food types, 2) they feed the most available foods to nestlings regardless of quality, or 3) they switch to low-quality, abundant foods only when natural food availability is low. Parents discriminated between natural and human-provided foods by showing a preference for natural foods when rearing young. When availability of natural foods was experimentally decreased, parents in both habitats switched to human-provided foods. However, the switch to human-provided foods was less pronounced in suburban parents suggesting a greater preference for natural foods. Regardless of preferences demonstrated at feeders, parents in both suburbs and wildlands delivered mostly natural foods to nestlings, independent of natural food availability. However, natural foods are likely to be scarcer in the environment than in our experimental tests. Because natural food availability is lower in the suburbs than in the wildland habitat, but brood sizes are similar, parents in the suburbs may be forced to switch to human-provided foods when feeding nestlings.

Introduction

With the worldwide-spread of human settlement, an increasing number of species has access to human-provided foods. Many mammal (Fedriani et al. 2001) and bird species (Marzluff 2001) feed on human-provided foods and access to this resource can change various aspects of a species' ecology and demography, e.g. home range, group size, density and survival (Fedriani et al. 2001, Marzluff 2001, Gilchrist and Otali 2002). Nevertheless, studies of the behavioral mechanisms leading to these changes are lacking. Unfortunately, the effects of human-provided foods cannot always be inferred from the many food supplementation studies conducted (for reviews see Martin 1987, Boutin 1990). Most experimental supplementations increase the total amount of food available but do not change the natural food availability in the environment, which may vary from year to year and from study to study. In contrast, in urban habitats human-provided foods increase, but natural food availability might decrease. Arthropods, for example, are likely to decrease in abundance in urbanized areas (McIntyre 2000). In general, urbanization can change the composition, quantity, quality, and the temporal and spatial pattern of overall food available (Annett and Pierrotti 1999).

In birds, food often is a limiting factor for reproductive success (Martin 1987). Hence, we might expect access to human-provided foods to increase reproductive success, which may be true in some bird species (Pons and Migot 1995, Marzluff 2001, Bertellotti et al. 2001). But some studies suggest that human-provided foods reduce reproductive success because of its lower quality for nestlings (Annett and Pierrotti 1999, Belant et al. 1998, Boal 1999). Most human-provided foods are plant-based and, as such, are harder to digest (Karasov 1990, Buchsbaum 1986, Jakubas et al. 1995) and often have a lower water content (e.g birdseeds, Diaz 1989) than animal foods. Nestlings have poorer digestive capabilities (Caviedes-Vidal and Karasov 2001) and greater water requirements than adults (Robbins 1983). Therefore, plants may not be of sufficient quality to maintain the fast growth rates characteristic for nestling passerines. In support, zebra finch nestlings (*Taeniopygia guttata)* grew more slowly on a plant-based diet than did control nestlings fed a natural mixed diet (Birkhead et al. 1999). However, studies on great (*Parus major*) and blue (*P. caerulescens*) tits (Cowie and Hinsley 1988) and on laughing gulls (*Larus atricilla*, Dosch 1997) in urban areas did not show a negative effect of human-provided foods on

nestlings. Hence, whether or not human-provided foods are of low quality for nestlings may depend on the type of human-provided foods and species-specific nutritional needs and digestive capabilities of nestlings.

The diet of adult Florida scrub-jays (*Aphelocoma coerulescens*) in suburban habitats consists of 30% human-provided foods (Fleischer et al. 2003). The consumption of these foods (mostly peanuts) does not seem to affect adults; few differences in adult body condition exist between jays in suburban and wildland habitats (Schoech and Bowman 2003). Although human-provided foods are available *ad libitum* in the suburban habitat, arthropod abundance is lower than in wildland habitat (Shawkey et al. 2004). Suburban nestlings have lower pre-fledging mass and post-fledging survival than their wildland counterparts (Bowman and Woolfenden, unpublished data), whom are fed almost exclusively animal foods, especially orthopterans and lepidopteran larvae (Stallcup and Woolfenden 1978). This suggests that nestling growth in the suburbs might be limited by the availability of arthropod food or by a negative effect of being fed human-provided foods. To explain higher rates of brood reduction in suburban habitats, Shawkey et al. (2004) suggested that suburban nestlings received less food and food that was of lower quality as compared to wildland nestlings.

Why do parents feed nestlings low-quality, human-provided foods in urban habitats if this decreases nestling survival? First, they may not be able to assess the quality of these novel food types (hypothesis 1). We experimentally tested for food discrimination between natural and human-provided foods by conducting food trials during three different periods when the nutritional demands differed. We assumed that if jays changed their preference when nutritional needs changed, they would be able to discriminate between food types. We predicted that, a) parents would show little preference for animal versus plant foods during the pre-breeding period. Both animal and plant foods (specifically acorns) are an important part of the pre-breeding diet (Woolfenden and Fitzpatrick 1996). We further predicted that, b) preference for natural foods would increase with the onset of breeding and this would occur earlier in females than in males. Nutritional demands change with the onset of breeding. During oogenesis, females require additional protein, fat, and selected micronutrients (Carey 1996, Ramsay and Houston 1997), which females acquire more easily through animal than plant-based food (Karasov 1990). We also predicted that c) the

preference for natural foods would be greatest during nestling rearing. Parents should feed nestlings easily and rapidly digested foods that are rich in protein.

Second, parents might feed human-provided foods to nestlings because they choose the most accessible food types, i.e., the foods with the lowest search and handling time, regardless of quality (hypothesis 2). Third, parents might be forced to switch to low-quality, abundant human-provided foods because of time and energy constraints on foraging for relatively scarce natural foods in the suburban habitat (hypothesis 3). Hypothesis 2 predicts that parents always choose the more accessible food type even if it is of low quality. Independent of habitat and natural food availability in the environment, they will choose low-quality, human-provided foods when the accessibility of natural foods is experimentally decreased. Hypothesis 3 predicts that parents will choose the more available low-quality food type only when natural food availability in the environment is low. Because natural food availability is lower in the suburban than the wildland habitat, suburban parents will be more likely to choose the low-quality food type with reduced accessibility of the high-quality food. For the food items taken to the nest, hypothesis 2 predicts that parents in both habitats will take the low quality food to the nest, when the accessibility of the high quality food is reduced. Hypothesis 3 predicts that only suburban parents will take the low quality food to the nest. We used a combination of supplemental feeding and food choice trials in two habitats that differ in natural food availability to test these hypotheses.

Methods

Study organism

Florida scrub-jay groups consist of a socially and genetically monogamous breeding pair and from zero to six non-breeding helpers. The birds breed cooperatively and defend year-round all-purpose territories. Males do not incubate the eggs or brood nestlings, but provide food to both the breeding female and young. Females brood young, but increase their provisioning rate throughout the later half of the nestling period. Helpers provide some food to nestlings and fledglings, and assist in nest defense (for references and further information on the species see Woolfenden and Fitzpatrick 1996). The Florida scrub-jay is the only bird species endemic to Florida and is federally listed as Threatened. At present,

over 30% of Florida scrub-jay populations occur in urban habitats (Breininger 1999). These populations all have year-round access to human-provided foods and most, if not all, appear to be declining.

Study population

We studied food preference of Florida scrub-jays in suburban and wildland habitats of Highlands County, Florida. The suburban study site was located at Placid Lakes Estates (27° 10'N, 81°24'W), a residential housing subdivision near Lake Placid (for details see Bowman and Woolfenden 2001, 2002). Here, the native scrub vegetation occurs as patches within a matrix of roads and human housing. The wildland study site is at Archbold Biological Station (for details see Mumme 1992, Schoech et al. 1996), approximately 10-12 km south of the suburban site. In this natural preserve the scrub vegetation is part of a heterogeneous landscape of periodically burned habitats, including xeric oak scrub, scrubby flatwoods, rosemary balds, and seasonal ponds (Abrahamson et al. 1984). All birds of both populations are individually color marked and the sex, social status (breeder, nonbreeder), and nest status (building, incubating, brooding) of each jay are known from ongoing long-term studies on the demography of the two populations (Schoech et al. 1996, Bowman and Woolfenden 2001).

Food discrimination (hypothesis 1)

In the first experiment, we tested whether parents discriminated between different food types and if both males and females changed food preferences with stage of breeding. This experiment was conducted between February 12th 2002 and June 13th 2002 in the suburban population only. The groups tested consisted of breeding pairs without helpers. We tested the birds in each territory up to three times: (1) pre-breeding: 1 to 2 weeks before the laying of the first egg (18 trials), (2) mid-incubation: day 9 of incubation (17 trials), (3) brooding: day 12 or 13 post-hatching (7 trials). Trials were performed 2 to 4 hours after sunrise. One to 3 days before each trial, a feeder was placed near the activity center of the territory during the pre-breeding phase and 10 to 20 m from the nest during the breeding phase and the jays were familiarized with all food types to avoid measuring the response to a novel food. The feeder consisted of a one-meter wooden pole, topped with a plastic

saucer (diameter 20 cm, Martha Stewart, New York). The foods offered were 60 waxworms (*Galleria mellonella*, Grubco, Hamilton, Ohio, appr. 36 kcal), 20 pieces of white wheat bread (appr. 2 kcal), 20 sunflower seeds (appr. 9 kcal) and 20 peanut pieces (appr. 25 kcal). The nutritional composition and caloric value of these foods are shown in Table 1. The human-provided foods (peanuts, bread, and sunflower seeds) were chosen to reflect foods available to the suburban jays and to match the total amount and caloric value of the waxworms, which were used as a surrogate for natural foods commonly fed to nestlings (lepidopteron larvae and other arthropod prey). Each trial started when the first bird landed on the table and ended when the birds had removed 20 items or after 45 minutes had elapsed. After 20 items, one food type could have been depleted, and therefore the birds would no longer have a choice among all four food types. Trials with fewer than five items taken by both birds were discarded. For each item taken, we recorded the food type and the individual that took it.

Following Alldredge and Ratti (1986), we used a Friedman test on the proportion of each food type taken per breeding stage to determine whether the food types were taken according to their availability. In addition, to determine which resources were preferred or avoided in each of the breeding stages, we calculated Bonferroni's simultaneous confidence intervals (Byers and Steinhorst 1984). Because in many of the trials sunflower seeds and bread were avoided completely, data were skewed preventing the use of analyses of variance. To determine if the number of waxworms taken by each group changed with the breeding stage, we used a Friedman test for related samples. Differences between the sexes were analyzed using a Mann-Whitney-U test for each breeding stage. Because females came to the feeder less often and took fewer items than males, we compared the proportion of natural items taken by males and females rather than the absolute number of items taken by each sex.

Food choice depending on food availability (hypotheses 2 and 3)

In the second experiment, we manipulated food availability in the environment by supplementing groups in both habitats with waxworms. Non-supplemented groups received no waxworms during this period. We performed this experiment between March 29th and May 26th 2003 using a design similar to the first experiment except that trials were

conducted in both the suburbs and wildlands. We tested groups regardless of group size. At hatching, groups in each study area were alternately assigned to the non-supplemented or supplemented treatment. Each day, between day 1 and 10 post-hatching, supplemented groups received 30 grams of waxworms. Non-supplemented groups received one peanut broken into pieces as a control for the disturbance of a researcher's visit near the nest. On day 11, we counted the number of nestlings per brood as an indicator of food demand.

Next, we conducted food trials similar to those conducted in the first experiment, but we experimentally manipulated the handling time of natural foods during one of the food trials (see below). Between days 12 and 17, we presented each group with a choice between 60 waxworms (13 grams, 36 kcal) and 60 pieces of peanuts (6.4 grams, 36 kcal). Choice trials were conducted twice for each group; during one of these trials, randomly allocated to first or second trial, we increased the handling time necessary to gather the waxworms from the feeder. We placed waxworms on a 3 x 50 cm corrugated cardboard strip, which we then rolled tightly. The waxworms were not deeper than 1 cm from the edge of the roll, i.e., easily within the reach of a scrub-jay beak. The roll was attached to the feeder using cable ties. Before the trials, jays in all groups were trained to extract the waxworms from the rolled cardboard. Trials were performed one to three hours after sunrise. Each trial started when the first bird landed on the table and ended when all items had been taken or after 45 minutes had elapsed. For each item taken, we recorded the identity and fate of the item. Fate was categorized as eaten at the feeder, carried away from the feeder to be eaten elsewhere or cached, or taken to the nest. For analyses of preference at the feeder we used only the first 60 items taken, because at this time all of a preferred item could have been depleted. For the analyses of the items taken to the nest, we used all items recorded because only 10 percent of all items where taken to the nest and birds could always choose whether or not to bring an item to the nest.

To test whether food preference depended on habitat, supplementation, brood size, or group size, we used a repeated-measures ANCOVA. Group identity was the subject, habitat and supplementation were the independent factors, brood size and group size were covariates, handling time (not manipulated / increased) was the within-subjects variable, and the logit-transformed proportion of waxworms taken was the dependent variable. We tested for the interaction between habitat and supplementation. For the analyses of the food

items taken to the nest, ANCOVA could not be applied because the assumption of homogeneity of variances was violated. We used Wilcoxon signed-rank tests to determine whether the proportion of waxworms taken to the nest differed from the proportion of waxworms taken from the feeder, and whether preference for waxworms depended on handling time. To test if the proportion of waxworms taken to the nest varied with habitat or food supplementation, we used a Mann-Whitney-U test. The analysis of the proportion of waxworms taken to the nest was done separately for waxworms with and without the handling time increase because data collected from the same group were not independent. We used two measures of food preference 1) the proportion of waxworms, i.e., number of waxworms divided by the number of all items taken per trial and 2) the strength of the response to the handling time treatment (see Whelan and Willson 1994). These authors assessed preference for different fruit types in the following manner. First, they let a bird choose between two fruits. Then, they decreased the availability of the preferred fruit and measured whether the preference of the bird was reversed. The strength of the food preference was measured as the interaction between food type and change in availability (handling time). In our study, we used the strength of the response (i.e., the difference in preference for natural foods between the not manipulated and increased handling time treatment per group) as a preference measure. The strength of preference is the within-subject effect in the repeated measures ANCOVA. No difference meant no diet switch and, therefore, a high preference. All statistical analyses were done using SPSS 11.5 for Windows (SPSS Inc, 2002).

Results

Food discrimination (hypothesis 1)

Florida scrub-jays discriminated among food types in all breeding stages (Fig. 1). During pre-breeding the use of the food types differed from their respective availability (Friedman test, $T= 20.66$, $df= 17$, $P< 0.01$). Waxworms were avoided, peanuts were preferred, and bread and sunflower seeds were taken according to their availability. During incubation, jays also discriminated among food types (Friedman test, $T= 7.42$, $df= 16$, $P< 0.01$). Waxworms, peanuts, and bread were taken according to their availability, but sunflower seeds were avoided. During nestling rearing, only seven groups were tested

because of a high rate of nest failures. Although the proportion of waxworms taken was higher than expected (0.74, expected: 0.50), and the proportion of bread (0.08, expected: 0.17) and sunflower seeds (0.00, expected: 0.17) taken were lower than expected, the differences were not significant, likely as a result of the relatively low sample sizes. Overall, as breeding advanced, birds took an increasing number of waxworms (Friedman test for related samples, N= 7, $\chi^2 = 5.85$, df= 2, P= 0.05) and a decreasing number of sunflower seeds (N= 7, $\chi^2 = 6.00$, df= 2, P= 0.05). The number of peanuts (N= 7, $\chi^2 = 1.87$, df= 2, P= 0.42) and bread items taken (N= 7, $\chi^2 = 4.44$, df= 2, P= 0.11) did not vary significantly with breeding stage. A difference existed between males and females in their preference for waxworms. During incubation, females showed an earlier preference for natural foods than males: females took a higher proportion of waxworms than males (means ± SD, 0.89 ± 0.15 vs. 0.47 ± 0.48 respectively; Mann-Whitney-U test, Z=-1.86, N= 23, one-tailed P= 0.03) as predicted, but during nestling rearing the proportions did not differ (0.85 ± 0.15 vs. 0.71 ± 0.42, respectively; Mann-Whitney-U test, Z= -0.00, N= 12, one-tailed P= 0.52).

Food choice depending on food availability (hypotheses 2 and 3)

We tested food choice in a total of 43 groups, 38 of them in both handling time treatments (not manipulated / increased handling time for waxworms). At the feeder, birds took more peanuts when handling time for waxworms was increased, even though this experiment was conducted during nestling rearing when waxworms were the main food item taken (Fig. 1). This was true for supplemented and non-supplemented groups in both habitats (Fig. 2, Table 2). In Table 2, between-subject effects refer to difference in preference for waxworms, whereas within-subject effects indicate differences in the degree of diet switching. Food supplemented birds took a higher proportion of waxworms (supplementation effect, Table 2), but did not show less diet switching than non-supplemented birds. Suburban birds chose a higher proportion of waxworms (habitat effect, Table 2) and switched their diet less than wildland birds. In addition, neither the proportion of waxworms taken nor the degree of diet switching depended on the interaction between habitat and supplementation, brood size, or group size. Thus, consistent with the predictions of hypothesis 2, birds switched diet in both habitats. Hypothesis 3 also was partially

supported; preference for waxworms was higher in supplemented than non-supplemented birds. However, contrary to the predictions of hypothesis 3, preference for natural foods was higher in the suburban than the wildland habitats.

Ten of 43 groups tested took items to the nest in both handling-time treatments. Preference for waxworms to feed nestlings did not depend on handling time (Figure 2b; Wilcoxon signed rank test, $Z= -0.420$, $N= 10$, $P= 0.67$). In further analyses, we analyzed the two handling time treatments separately because of statistical considerations (see methods). The results were identical for both treatments. The proportion of waxworms taken to the nest was higher than the proportion of waxworms taken from the feeder (Wilcoxon signed ranks test, not manipulated handling time: $Z= -3.668$, $N= 27$, $P< 0.01$, increased handling time: $Z= -3.668$, $N= 27$, $P< 0.01$), i.e. a waxworm taken from the feeder was more likely to be fed to the nestlings than a peanut taken from the feeder. The proportion of waxworms taken to the nest did not differ between sites (Mann-Whitney-U test, not manipulated handling time: $Z= -1.118$, $N= 27$, $P= 0.35$, increased handling time: $Z= -0.176$, $N= 25$, $P= 0.89$) nor between non-supplemented and supplemented groups (Mann-Whitney-U test, not manipulated handling time: $Z= -0.176$, $N= 27$, $P= 0.894$, increased handling time: $Z= -0.205$, $N= 25$, $P= 0.85$). In general, the items taken to the nest consisted of more than 80 % waxworms in both habitats and all treatments. Thus, neither hypothesis 2 nor hypothesis 3 was supported. Adults preferred to feed nestlings waxworms, a surrogate for natural foods, in both habitats. This was the case even when they had to work harder to obtain the waxworms because of our experimental manipulation.

Discussion

Our results show that parents are able to discriminate between human-provided and 'natural' foods and adjust their preferences according to the differing nutritional demands of breeding. In the first experiment, they avoided sunflower seeds and bread and, with the onset of breeding, exhibited decreased preference for peanuts and an increased preference for waxworms. In the second experiment, they showed a strong preference for feeding waxworms to nestlings. We can thus refute the hypothesis that scrub-jays feed human-provided foods to nestlings because they can not discriminate between those foods and natural foods. All the human-provided foods are of plant origin and jays do not normally

feed plant foods to their nestlings (Stallcup and Woolfenden 1978). Thus, they may be preadapted to differentiate between animal and plant foods.

The food choices of parents support hypothesis 2; jays choose the most readily available foods when they need to meet only their own nutritional needs. When handling time for natural foods was increased, birds switched to the low-quality but more available human-provided food type regardless of habitat or whether they were food supplemented. In contrast, the food choices exhibited when jays were feeding young do not support this hypothesis; jays did not feed the most readily available foods to nestlings. In fact, 80% of the items taken to the nest were waxworms, even when the handling time for waxworms was increased experimentally. The preference for natural foods to feed young, as compared with food choices for self-feeding, likely reflect the different nutritional needs of nestlings and adults. Nestlings grow rapidly (Starck and Ricklefs 1998) and have immature guts, hence extract fewer nutrients than adults (Karasov 1990), and are more likely to suffer from the consumption of low-quality foods than are their parents.

The food choices of parents at the feeder offer some support for hypothesis 3, and suggest that food preference and diet switching depend on time and energy constraints. In non-supplemented control groups, where natural food availability was lower than in supplemental groups, the preference for natural foods was less strong and birds were more likely to switch to low-quality foods when handling rates were increased. However, contrary to the prediction of hypothesis 3, suburban birds showed a greater preference for natural foods than wildland birds, despite the lower availability of natural foods in that habitat. Suburban birds were more likely to choose waxworms, even if the handling time for this food type had been increased. In addition, the food choices of parents when feeding young did not depend on natural food availability. The proportion of waxworms taken to the nest did not vary relative to supplementation or habitat. Alternately, if the nutritional demands of suburban adults are easily met because of the availability of human-provided foods, they might increase their efforts to provide nestlings with preferred food items. Fleischer et al. (2003) reported that the foraging efficiency of suburban scrub-jays was greater than that of wildland birds. Additionally, food supplemented blue tits (*Parus caeruleus*) exhibited increased food selectivity and brought larger items to the young than did control birds (Grieco 2001).

None of our hypotheses completely explained why suburban Florida scrub-jays feed human-provided foods to nestlings. Despite our experimental results, it is clear from observations during the breeding season, that jays feed nestlings human-provided foods in the suburbs. Our handling time treatment may not have been comparable to the increased searching times necessary for suburban jays to find arthropods in those habitats. Our experimental treatment may have added only 1 to 2 seconds to the handling times necessary to obtain waxworms. Despite that small increase, adults switched their own diet from waxworms to peanuts, although they continued to feed nestlings mostly waxworms. In suburban habitats, the abundance of arthropods per oak stem is less than half that in the wildlands (Shawkey et al. 2004) and fewer oak stems exist because of loss of the native scrub habitats. Optimal foraging models for foragers that take more than one prey type to a central place predict that selectivity for a preferred food decreases with decreased encounter rates with the preferred food (Houston 1985). When the encounter rate with the high-quality food type relative to the low-quality food type decreases, it should be adaptive to include the low-quality food type into the diet.

In general, the ecological conditions in the suburban habitat of reduced availability of preferred and high-quality arthropods and increased availability of less preferred and lower quality human-provided foods might result in parents providing nestlings with human-provided foods. This is especially true given the number of changes that occur with urbanization that might influence provisioning behavior. First, suburban birds breed earlier and lay larger clutches than wildland jays (Bowman and Woolfenden, unpublished data), thus suburban jays may have a relatively large mean brood size given the environmental quality of the suburbs. Food selectivity can decrease when brood demand is unexpectedly high (Wright et al. 1998). Second, in urban areas, the density of both birds and potential predators may be higher than in wildland habitats (see Kjoss and Litvaitis 2001, Haskell et al. 2001). An increase in the perceived risk of predation decreased food selectivity in the gila woodpecker (*Melanerpes uropygialis,* Martindale 1982) and, in our suburban study area, predation risk increases with human density (Thorington and Bowman 2003). Third, intra-specific interactions might affect provisioning behavior. Pre-breeding suburban scrub-jay females engage in more intra-specific territorial interactions than wildland females (Fleischer et al. 2003). Nevertheless, we do not know whether suburban parents invest more

time in intra- and inter-specific interactions during nestling rearing than wildland jays. Fourth, suburban groups have fewer helpers than wildland groups (Bowman, unpublished data). The lack of helpers in suburban groups also might contribute to time limitation of suburban birds, because helpers feed nestlings and engage in territorial defense (Stallcup and Woolfenden 1978). Because of potential time constraints and the reduced availability of preferred foods, suburban jays might not be able to fulfill the demands of their broods, and, consequently, decrease food selectivity.

Even in our experimental trials, 10% of the items fed to nestlings were human-provided foods. This small proportion of lower-quality foods might be sufficient to significantly reduce diet quality. Other studies have shown that nestling growth can be highly susceptible to variation in protein (e.g. Japanese quail, *Coturnix coturnix japonica*, Marks 1993) and fat content (e.g. house martin, *Delichon urbica*, Johnston 1993). Bird seed contains 3-12% water (Diaz 1989), while an average insect contains 70-75% water (Bell 1990). Suburban nestlings also might be more prone to dehydration and more susceptible to its effects because ambient temperatures are higher in the suburban habitat than in the wildlands (Kalnay and Cay 2003, LeClair and Bowman, unpublished data). In another experiment on jays at our natural site, Reynolds et al. (2003) found that food supplemented wildland females increased the amount of water but not fat allocated to eggs, indicating that water is a critical resource for nestling development.

In summary, scrub-jays clearly discriminate between high- and low-quality foods, but their preferences change, likely depending on seasonal nutritional demands. When the availability of preferred, high-quality foods is experimentally decreased, adults switch to lower-quality foods that are readily available; however, this is true only when self-feeding. When feeding nestlings, jays attempt to feed mostly arthropods. Despite this preference, suburban birds still fed their nestlings 10% human-provided foods. Outside of our experiments, we believe this proportion to be even higher. Relatively large brood sizes and reduced arthropod abundance may decrease the food selectivity of adult jays so that they can meet the demands of the brood. Consistent with optimal foraging theory, they include lower-quality foods in the nestlings' diet, even without changing their preference for high-quality arthropods. This study shows further that it is difficult to predict the behavioral responses to urbanization, because urbanization changes a variety of habitat characteristics

at the same time and these characteristics might interact. This study suggests that the increased availability of human-provided foods and the decreased availability of natural foods influence food choices in the suburban habitat.

Acknowledgements

We thank numerous research assistants, students and interns that helped in the field, especially K. Smith and J.W. Atwell. This manuscript benefited from the comments of D. Levitis, S.J. Reynolds, and A. Weidt. AS was supported by a graduate research internship at Archbold Biological Station, and by the American Ornithologists' Union, Basler Stiftung für biologische Forschung, DeGiacomi Foundation, Florida Ornithological Society, Janggen-Pöhn Foundation, Roche Research Foundation, and Wolfermann-Nägeli Foundation. Research in the suburban and wildland sites was supported by NSF grants IBN-0077469 and -0346557 to RB and grants IBN-9983201, -0235821, and -0346328 to SJS. All research on this listed species was permitted by the US Fish and Wildlife Service (permit TE824723-5 to Reed Bowman).

References

Abrahamson, W. G., A. F. Johnson, J. N. Layne, and P. A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. Florida Scientist **47**:209-250.

Alldredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management **50**:157-165.

Annett, C. A., and R. Pierrotti. 1999. Long-term reproductive output in Western Gulls: consequences of alternate tactics in diet choice. Ecology **80**:288-297.

Belant, J. L., S. K. Ickes, and T. W. Seamans. 1998. Importance of landfills to urban-nesting herring and ring-billed gulls. Landscape and Urban Planning **43**:11-19.

Bell, G. P. 1990. Birds and mammals on an insect diet: a primer on diet composition analysis in relation to ecological energetics. Studies in Avian Biology **13**:416-422.

Bertellotti, M., P. Yorio, G. Blanco, and M. Giaccardi. 2001. Use of tips by nesting Kelp Gulls at a growing colony in Patagonia. Journal of Field Ornithology **72**:338-348.

Birkhead, T. R., F. Fletcher, and E. J. Pellatt. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. Proceedings of the Royal Society of London Series B **266**:385-390.

Boal, C. W., and R. W. Mannan. 1999. Comparative breeding ecology of Cooper's Hawks in urban and exurban areas of southeastern Arizona. Journal of Wildlife Management **63**:77-84.

Boutin, R. B. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. Canadian Journal of Zoology **68**:203-220.

Bowman, R., and G. E. Woolfenden. 2001. Nest success and the timing of nest failure of Florida Scrub-Jays in suburban and wildland habitats. Pages 383-402 *in* J. M. Marzluff, R. Bowman, and R. E. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, New York.

Bowman, R., and G. E. Woolfenden. 2002. Nest site selection by Florida Scrub-Jays in natural and human-modified habitats. Wilson Bulletin **114**:128-135.

Breininger, D. R. 1999. Florida Scrub-Jay Demography and Dispersal in a Fragmented Landscape. Auk **116**:520-527.

Buchsbaum, R., J. Wilson, and I. Valiela. 1986. Digestibility of plant constituents by Canada geese and Atlantic brant. Ecology **67**:386-393.

Byers, C. R., and R. K. Steinhorst. 1984. Clarification of a technique for analysis of utilization-availability data. Journal of Wildlife Management **48**:1050-1053.

Carey, C. 1996. Female reproductive energetics. Pages 375-416 *in* C. Carey, editor. Avian energetics and nutritional ecology. Chapman Hall, New York.

Caviedes-Vidal, E., and W. H. Karasov. 2001. Developmental changes in digestive physiology of nestling house sparrows, Passer domesticus. Physiological and Biochemical Zoology **74**:769-782.

Cowie, R. J., and S. A. Hinsley. 1988. Feeding Ecology of Great Tits (*Parus major*) and Blue Tits (*Parus caeruleus*), Breeding in Suburban Gardens. Journal of Animal Ecology **57**:611-626.

Diaz, M. 1989. Interspecific patterns of seed selection among granivorous passerines: effects of seed size, seed nutritive value and bird morphology. Ibis **132**:467-476.

Dosch, J. J. 1997. Diet of nestling Laughing Gulls in Southern New Jersey. Colonial Waterbirds **20**:273-281.

Fedriani, J. M., T. K. Fuller, and R. M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography **24**:325-331.

Fleischer, A. L., R. Bowman, and G. E. Woolfenden. 2003. Variation in foraging behavior, diet and the time of breeding of Florida Scrub-Jays in suburban and wildland habitats. Condor **105**:515-527.

Gilchrist, J. S., and E. Otali. 2002. The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose. Canadian Journal of Zoology **80**:1795-1802.

Grieco, F. 2001. Short-term regulation of food-provisioning rate and effect on prey size in blue tits, *Parus caeruleus*. Animal Behaviour **62**:107-116.

Haskell, D., A. M. Knupp, and M. C. Schneider. 2001. Nest predator abundance and urbanization. Pages 243-258 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Norwell, MA.

Houston, A. I. 1985. Central place foraging: some aspects of prey choice for multiple-prey loaders. American Naturalist **125**:811-826.

Jakubas, W. J., C. G. Guglielmo, C. Vispo, and W. H. Karasov. 1995. Sodium balance in ruffed grouse as influenced by sodium levels and plant secondary metabolites in quaking aspen. Canadian Journal of Zoology **73**:1106-1114.

Johnston, R. D. 1993. Effects of diet quality on the nestling growth of a wild insectivorous passerine, the House Martin *Delichon urbica*. Functional Ecology **7**:255-266.

Kalnay, E., and M. Cai. 2003. Impact of urbanization and land-use change on climate. Nature **423**:528-531.

Karasov, W. H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. Studies in Avian Biology **13**:391-415.

Kjoss, V. A., and J. A. Litvaitis. 2001. Community structure of snakes in a human-dominated landscape. Biological Conservation **98**:285-292.

Marks, H. L. 1993. The Influence of Dietary-Protein Level on Body-Weight of Japanese-Quail Lines Selected under High-Protein and Low- Protein Diets. Poultry Science **72**:1012-1017.

Martin, T. E. 1987. Food as a Limit on Breeding Birds - a Life-History Perspective. Annual Review of Ecology and Systematics **18**:453-487.

Martindale, S. 1982. Nest defense and Central Place Foraging: A Model and Experiment. Behavioral Ecology and Sociobiology **10**:85-89.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19-48 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwall, MA

McIntyre, N. E. 2000. Ecology of urban arthropods: A review and a call to action. Annals of the Entomological Society of America **94**:825-835.

Mumme, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. Behavioral Ecology and Sociobiology **31**:319-328.

Pons, J.-M., and P. Migot. 1995. Life-history strategy of the herring gull: changes in survival and fecundity in a population subjected to various feeding conditions. Journal of Animal Ecology **64**:592-594.

Ramsay, S. L., and D. C. Houston. 1997. Nutritional constraints on egg production in the blue tit: a supplementary feeding experiment. Journal of Animal Ecology **66**:649-657.

Reynolds, S. J., S. J. Schoech, and R. Bowman. 2003. Nutritional quality of prebreeding diet influences breeding performance of the Florida scrub-jay. Oecologia **134**:308-316.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Academic Press, Orlando.

Schoech, S. J., and R. Bowman. 2003. Does differential access to protein influence differences in timing of breeding of Florida Scrub-Jays (*Aphelocoma coerulescens*) in suburban and wildland habitats? Auk **120**:1114-1127.

Schoech, S. J., R. L. Mumme, and J. C. Wingfield. 1996. Prolactin and helping behaviour in the cooperatively breeding Florida scrub-jay, *Aphelocoma c. coerulescens*. Animal Behaviour **52**:445-456.

Shawkey, M. D., R. Bowman, and G. E. Woolfenden. 2004. Why is brood reduction in Florida scrub-jays higher in suburban than in wildland habitats? Canadian Journal of Zoology **82**:1427-1435.

Stallcup, J. A., and G. E. Woolfenden. 1978. Family status and contributions to breeding by Florida Scrub Jays. Animal Behaviour **26**:1144-1156.

Starck, J. M., and R. E. Ricklefs. 1998. Avian growth and development: evolution within the altricial-precocial spectrum. Oxford University Press, New York.

Thorington, K. K., and R. Bowman. 2003. Predation on artificial nests increases with human housing density in suburban habitats. Ecography **26**:188-196.

Whelan, C. J., and M. F. Willson. 1994. Fruit Choice in Migrating North-American Birds - Field and Aviary Experiments. OIKOS **71**:137-151.

Woolfenden, G. E., and J. W. Fitzpatrick. 1996. Florida Scrub-Jay *(Aphelocoma coerulescens)*. Pages 1-28 *in* A. Poole, editor. The Birds of North America. American Ornithologists' Union and The Academy of Natural Sciences, Philadelphia.

Wright, J., E. Berg, S. R. de Kort, V. Khazin, and A. A. Maklakov. 2001. Safe selfish sentinels in a cooperative bird. Journal of Animal Ecology **70**:1070-1079.

Table 1: Nutritional composition of food types in the food preference experiment

Item	Moisture	Fat	Protein	Kcal/g	Kcal/item	Source
Waxworm	61.73 %	22.19 %	15.50 %	2.77	0.60	Grubco 2004[1)]
Peanut	6.50 %	49.23 %	25.80 %	5.67	1.25	About 2004[2)]
White bread	36.70 %	3.60 %	8.20 %	0.17	0.45	About 2004[2)]
Sunflower seeds (seed kernel)	1.20 %	49.80 %	19.32 %	5.82	0.10	About 2004[2)]

[1)] www.grubco.com, [2)] http://nutrition.about.com/library/foodfind/

Table 2: Repeated measures univariate analyses of variance for the proportion of waxworms taken per trial depending on waxworm handling time, habitat, supplementation, brood size and group size. We removed the non-significant handling time * habitat * supplementation interaction.

Source	Type III Mean Square	df	F	P
Within-subject effects				
Handling time	7.789	1	8.215	0.007
Handling time * habitat	4.879	1	5.146	0.030
Handling time * supplementation	2.524	1	2.662	0.112
Handling time * brood size	0.087	1	0.092	0.764
Handling time * group size	2.420	1	2.553	0.120
Error (treatment)	0.948	33		
Between-subject effects				
Habitat	5.319	1	3.638	0.065
Supplementation	7.827	1	5.353	0.027
Brood size	0.205	1	0.140	0.711
Group size	1.892	1	1.294	0.264
Error (treatment)	1.462	33		

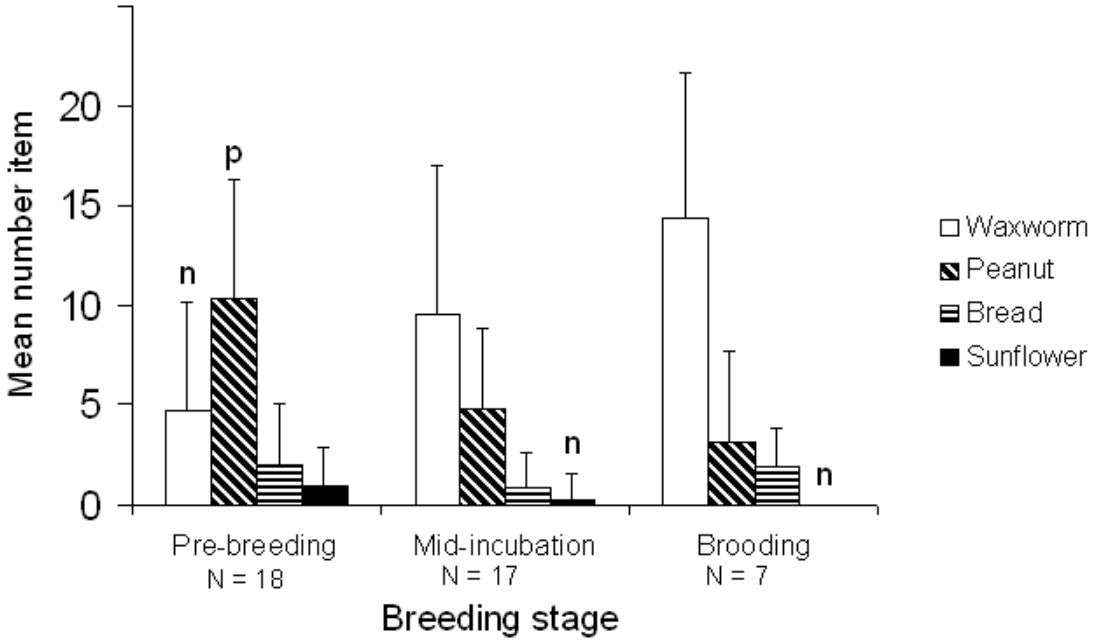

Figure 1: Mean number (± SD) of each food type taken per breeding stage. 'p' indicates positive selection, 'n' indicates negative selection, no sign indicates no selection determined by Bonferroni's simultaneous confidence intervals. N= number of groups tested.

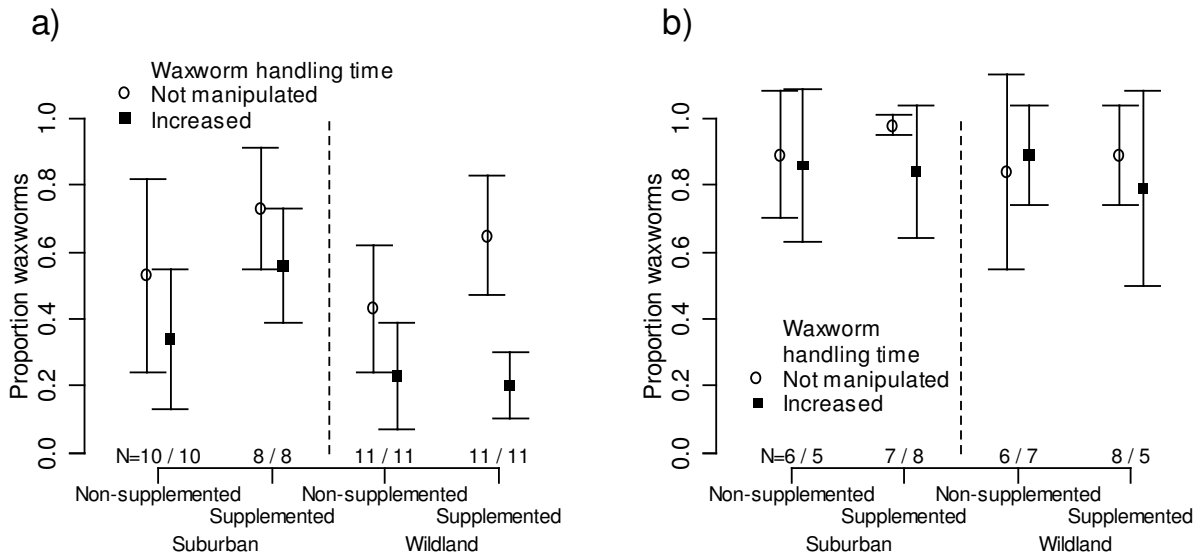

Figure 2: Proportion of waxworms (natural food, ± SD) a) taken at the feeder and b) taken to the nest depending on habitat, supplementation and waxworm handling time. N= number of groups tested. N are smaller in items taken to the nest (2b) than taken at the feeder (2a), because birds did not take food to the nest in all groups.

CHAPTER 4

Parental time budgets and human-provided foods as nestling diet in Florida scrub-jays: evidence for food or time limitation?

Annette Sauter

Abstract

As urbanization spreads worldwide an increasing number of species has access to human-provided foods. The availability of this novel food type may influence foraging behavior and reproductive success of urban birds and may be one of the main factors shaping urban bird communities. In suburban habitats, Florida scrub-jays breed earlier and have larger clutch sizes than wildland jays, but their nestlings have reduced growth and survival, probably because parents feed their nestlings some human-provided foods rather than a strict diet of arthropods, as they do in the wildlands. I observed parental foraging behavior in the wildland and suburban habitat to: (1) investigate whether habitat-specific differences in parental behavior and food capture rates indicate food or time limitation for foraging within suburban habitats that could explain why suburban parents feed plant matter to nestlings despite the apparent costs of doing so; and (2) determine the relative importance of plant foods in the nestling diet in both habitats. Apart from increased nest attendance in the suburban habitat, I observed no difference in parental behavior between the habitats. On the other hand, suburban parents captured more arthropods and plant items per unit foraging time than wildland birds. Hence, I found no evidence for food or time limitation for foraging of the parents. Wildland parents delivered only animal foods to their nestlings, whereas 15% of the foods delivered to nestlings in the suburbs were plant-based human-provided foods indicating a partial preference for plant foods in the suburban habitat. I discuss possible mechanisms by which the availability of human-provided foods can lead to the observed partial preference for plant foods.

Introduction

Human settlements are spreading worldwide and consequently more animal species live in urban habitats and have access to human-provided foods. In urban habitats, human-provided foods often are the most abundant food year-round while natural food sources, such as arthropods (McIntyre 2000) and some small mammals (Dickman and Doncaster 1987), tend to decline or are only available seasonally. As food availability changes, so does the foraging behavior of urban birds (e.g. Fernandez-Juricic 2000), and other animals (e.g. Bowers 1996). In addition to their natural diet, urban birds exploit novel food types and foraging habitats, such as seed from feeders, nectar from exotic vegetation, and human refuse from garbage dumps (Marzluff 2001, French et al. 2005). Furthermore, urban birds often forage very efficiently because humans provide predictable and abundant food sources (Shochat et al. 2004). Changes in foraging behavior can affect local population dynamics because foraging success, and behaviors that mediate it, influence fitness (Blanckenhorn 1991). In support, the demographic success of many urban species increases with the consumption of human-provided foods (Clergeau et al. 1998, Fedriani et al. 2001, Marzluff 2001, but see Dosch 1997, Annett and Pierrotti 1999). However, increased demographic success in urban habitats may be caused by other ecological changes that accompany urbanization, such as decreased predation risk (Marzluff 2001).

Suburban populations of Florida scrub-jays (*Aphelocoma coerulescens*), a corvid endemic to Florida, have decreased demographic success (Breininger 1999, Bowman, unpublished data), despite access to and consumption of human-provided foods (Fleischer et al 2003). At present, over 30% of all Florida scrub-jays occur in suburban habitats (Breininger 1999). About 30% of the diet of pre-breeding suburban females is human-provided, and consists mostly of peanuts (*Arachis hypogeae*), bird seed and bread (Fleischer et al. 2003). The mass and overall condition of suburban and wildland adults does not differ pre-breeding, but suburban females have higher levels of plasma protein than wildland females, possibly because they have access to protein-rich human-provided peanuts (Schoech and Bowman 2003). These patterns suggest that human-provided foods are adequate or even relatively high-quality for adults. Access to high-quality supplemental food often advances timing of breeding (Aparicio and Bonal 2002, Boutin 1990) and suburban birds breed earlier and lay larger clutches than do wildland birds (Bowman et al. submitted). In contrast, the growth and survival of suburban nestlings is lower than their

wildland counterparts (Shawkey et al. 2004), possibly as a result of decreased quantity or quality of their diet. Suburban nestlings are fed human-provided plant foods (Shawkey 2001), but wildland nestlings are fed only animal foods (Stallcup and Woolfenden 1978). Plant foods may inhibit nestling growth rates as found in zebra finch (*Taeniopygia guttata*) nestlings (Birkhead et al. 1999). Nevertheless, the importance of plant foods in the diet of nestling suburban jays has not yet been studied.

Suburban parents may include plant foods in the diet of nestlings for the following five reasons. First, they may not be able to discriminate against human-provided foods. However, in food choice experiments during nestling rearing suburban parents showed a strong preference for feeding arthropods to nestlings and discriminated against human-provided foods (Sauter et al. unpublished, chapter 3). Second, although human-provided foods may be less preferred, suburban parents may include them in the nestling diet because they are food limited themselves (Markman et al. 2002). Adult jays in the suburbs seem to easily fulfill their own nutritional needs and, when not providing food to nestlings, forage more efficiently than jays in the wildlands, likely because of the spatial and temporal predictability of human-provided food (Fleischer et al. 2003). Third, adult jays prefer to feed nestlings arthropods rather than human-provided foods (Sauter et al. unpublished, chapter 3), but the abundance of arthropods, especially lepidopteran larvae, in patches of native habitat is lower in the suburbs than in the wildlands (Shawkey et al. 2004). Suburban parents may feed nestlings human-provided foods because of the increased cost of finding scarce arthropods when the brood demand is high (Houston 1985). Fourth, although brood sizes are the same in both suburban and wildland habitats, if the availability of arthropods is reduced in the suburbs, then brood demand may be high relative to the preferred resources available for raising young. Although jays forage more efficiently in the suburbs, they might not be able to gain enough additional energy from human-provided foods to compensate for the increased searching time needed to find scarce arthropods. In support, suburban parents chose more human-provided foods when the handling time for natural foods was experimentally increased than when human-provided and natural foods were equally available (Sauter et al. unpublished, chapter 3). Fifth, suburban parents might invest more heavily in activities other than foraging such as territory defense. Fleischer et al. (2003) found that pre-breeding suburban females defended their territory more often than did wildland females, possibly because overall jay density is higher and territory size

smaller in the suburbs. In addition, fewer breeding pairs have helpers in the suburbs than in the wildlands (Bowman, unpublished data). Helpers feed nestlings and engage in territorial defense, including taking turns as 'sentinels' (Mumme 1992), thus potentially enabling parents to devote additional time to providing resources to nestlings.

I observed the foraging behavior of parents and their helpers in the wildland and suburban habitats to investigate whether differences in food capture rates and time budgets between habitats might help explain why suburban parents feed human-provided plant-based foods to their nestlings. My hypotheses were that (1) suburban parents have a lower capture rate with animal foods and a higher capture rate with plant foods than wildland parents; (2) capture rates with animal foods are lower in human-modified than in native habitat patches within the suburban habitat; and (3) suburban parents avoid foraging in human-modified patches. I further hypothesized that (4) suburban parents spend more time in defense behaviors instead of foraging and consequently capture fewer animal food items than wildland parents. Second, I wanted to determine the importance of plant foods in the nestling diet in both habitats. I hypothesized that (5) suburban nestlings receive more plant foods than wildland nestlings even though parents prefer feeding animal foods to nestlings. I predicted that 1) suburban parents bring plant foods to the nest, while wildland parents do not and that 2) suburban parents take a smaller proportion of plant items to the nest than they encounter or capture while foraging.

Methods

Study organism

Florida scrub-jay groups consist of a socially and genetically monogamous breeding pair and from zero to six non-breeding helpers (Woolfenden and Fitzpatrick 1984, 1996). The birds breed cooperatively and defend year-round all-purpose territories. Male Florida scrub-jays do not incubate or brood nestlings, but provide food to both the breeding female and nestlings. Females incubate, brood and feed nestlings. Helpers provide some food to nestlings and fledglings, and assist in nest defense.

Study areas

I studied the behavior of Florida scrub-jays in suburban and wildland habitats of Highlands County, Florida. The suburban study site was located at Placid Lakes Estates

(27° 10'N, 81°24'W), a residential housing subdivision near Lake Placid (for details see Bowman and Woolfenden 2001, 2002). Here, the native scrub vegetation occurs as patches within a matrix of roads and human housing. The wildland study site was located at Archbold Biological Station (27° 10' N, 81° 21'W, for details see Mumme 1992, Schoech et al. 1996). In this natural preserve the scrub vegetation is part of a heterogeneous landscape of periodically burned habitats, including xeric oak scrub, scrubby flatwoods, rosemary balds, and seasonal ponds (Abrahamson et al. 1984). Human-provided foods are available in the suburbs year-round. Wildland scrub-jays occasionally receive peanut bits by researchers and visitors, but the amount they receive is considered inconsequential for their energy budget (Fleischer et al. 2003). All birds of both populations are individually color marked and the sex, social status (breeder or non-breeder), and nest status (building, incubating, nestling) of each jay is known from ongoing long-term studies on the demography of the two populations (Woolfenden and Fitzpatrick 1984, Bowman and Woolfenden 2001).

Observations

I conducted focal watches (see below) on breeding and non-breeding members of Florida scrub-jay groups that were rearing nestlings in suburban and wildland habitat between March 26 and May 29, 2004. All birds were observed at peak times for foraging activity and nestling feeding (Stallcup and Woolfenden 1978), between 0.5 hours and 3 hours after sunrise, and between 3 hours and 0.5 hours before sunset. I recorded the behavior of a focal individual for one hour using a combination of instantaneous sampling and continuous recording (Martin and Bateson 1986) with field glasses (10× magnification). Each one-hour focal watch was divided into 30 second sampling units. At the end of each sampling unit, I determined the instantaneous behavior and the type of habitat patch of the focal bird. The instantaneous behaviors included flight, foraging, foraging out of sight, territory defense, on nest, sentinel, perched and out of sight. I adopted the behavioral definitions of DeGange (1976) with slight modifications. Preening and other maintenance activities were pooled with perching. Instead of female brooding, I used 'on nest' for all group members. I added chases and aggressive encounters with other bird species and mobbing terrestrial predators (Francis et al. 1989) to the territory defense. Foraging was divided into foraging and foraging out of sight. A bird was considered

foraging out of sight when it was not seen but heard to be moving through the vegetation at the sampling point, and was foraging in sight within 20 seconds before or after the instantaneous sample. Because birds are very secretive about going to the nest but are easily detected leaving the nest (pers. observation), I recorded the nest visitation rate as the number of times the bird left the nest per observation hour. The habitat patch was classified as unaltered native (open sand, *Quercus* sp., *Lyonia* sp., *Palmetto* sp., *Pinus* sp., rosemary *Ceratiola ericoides*) or human-modified (roads, road side, lawns, cleared lots, houses, vegetation in yards or on cleared lots). I was always more than 10 m away from the nest to avoid eliciting nest defense behavior.

To determine the diet of nestlings and the capture rates of individual food items, I continuously recorded identity and fate of each food item captured and the patch type from which the item was taken. Each of the food items was assigned to one of the three categories, animal, plant, or unknown. I noted the fate of each food item as eaten, cached, taken to the nest, or unknown. I assumed items were taken to the nest when they were placed in their esophageal pouch and the bird flew to the nest with the items remaining in the pouch. To estimate food capture rates for each individual, I calculated the mean number of items found and captured per minute foraging while in sight of the observer.

I performed up to three focal watches on each group, when nestlings were between 5 and 11 days old. Observations on the same group were alternated between mornings and afternoons and were conducted on different days. In groups without helpers, I performed one observation on the breeding female and two observations on the breeding male in random order. Males contribute most to nestling feeding (Stallcup and Woolfenden 1978) and, hence, I expected more variation in male behavior between the habitats. In groups with helpers, I observed one bird of each status (male, female, helper) in random order. Twenty-eight males were observed twice and 84 individuals (males, females or helpers) observed once. These individuals were members of 25 groups in the suburban and 24 groups in the wildland habitat. In all cases, I knew the location of the nest and the group structure; the focal individual was randomly selected before visiting the territory. To determine the proportion of human-modified and unaltered native habitat patches in each jay territory, territories were mapped in May 2004 following the method of Woolfenden and Fitzpatrick (1984). I modified digital orthoquads from aerial photos taken of the study site in 2000, by adding sites modified by humans since 2000. I calculated the proportion of human-

modified patches in each suburban territory by overlapping territory maps with the digital orthoquads in ArcView 3.3. (ESRI Inc. 1992-2002) using the above patch classification (unaltered or human-modified).

Variables used in the analyses

I excluded from the analysis all observations where the focal individual was out of sight for more than 30 minutes and observations of groups observed only once because of nest failure. To calculate time budgets, I combined focal watches performed on the same individual, summed the number of sampling units for each individual, and divided the number of sampling units in which a behavior occurred by the total number of sampling units, excluding unknown behavior for each individual. Apart from the description of mixed models, I report tests used in the results. I compared brood size and the proportion of groups with and without helpers between the habitats. For the brood size analysis I pooled the two broods containing one nestling with the 11 broods containing two nestlings and the 17 broods containing four nestlings with the one brood containing five nestlings.

Food capture rates and foraging patch selection: I tested for differences in capture rates of plant, animal and unknown items in all patches combined and in unaltered native vegetation between the suburban and wildland groups. Within suburban groups, I looked for a difference between: a) the capture rates of animal, plant and unknown food items of suburban birds in human-modified patches and unaltered patches; and b) the proportion of time spent foraging in human-modified patches relative to the proportion habitat comprised of human-modified patches in each territory. The sampling unit was the mean of all group members (males, females and helpers).

Parental time budget: To determine whether suburban males and females are time limited for foraging, I analyzed whether time budgets and foraging success of the breeding pair differed with helper presence and between habitats. I considered territory defense, sentinel and on nest as defense behaviors (Hailman and Woolfenden 1985, Woolfenden and Fitzpatrick 1996) and analyzed differences in the mean proportion of time spent in these behaviors between suburban and wildland groups. I analyzed territory defense using a non-parametric test. The proportion of time males and females spent on the nest, on sentinel, foraging (sum of foraging in sight and foraging out of sight), and the number of items found per observation hour were used as dependent variables in mixed models (proc mixed,

SAS, SAS Institute Inc. 2001). I used the number of items found per observation hour following Fleischer et al. (2003) as dependent variable to assess whether the time spent foraging directly relates to the number of items captured. Habitat (suburbs, wildland), sex (male, female), and the presence of helpers (no, yes) were categorical factors. Helper presence was coded as categorical factor because only 10 out of 49 groups had more than one helper. I entered helper presence as a factor instead of using helper behavior as a dependent variable, because this analysis allowed comparing female and male behavior. The square-root transformed brood size was the covariate. The group identity was a random factor to control for non-independence of males and females within the group. I initially included all two-way interactions, but removed the non-significant ones to build the final model.

In addition, I compared the mean number of animal items captured per observation hour of each group. I also tested for differences in the proportion of time spent in territorial behavior, on the nest, on sentinel, foraging, total number of items found per observation hour, number of items and proportion of plant versus other items taken to the nest between suburban and wildland helpers.

Nestling diet: I expected that suburban parents would bring more plant items to the nest than wildland parents. I determined if differences occurred in nest visitation rates and in the proportion of plant items taken to the nest between the habitats. Within the suburban groups, I tested for preference or avoidance for taking plant versus animal foods to the nest relative to capture rates, and for taking human-provided foods over acorns to the nest. Human-provided foods are encountered almost exclusively in the suburban habitat, but acorns are a plant food captured in both habitats (Fleischer et al. 2003). I compared: (a) the proportion of plant / all plant and animal items taken to the nest and the proportion of plant / all plant and animal items captured; and (b) the proportion of human-provided foods / acorns taken to the nest and the proportion of human-provided foods / acorns captured. In addition, I determined if the suburban groups that took plant items to the nest differed from those suburban groups that delivered only animal items in the frequency of helper presence, brood size, the time spent foraging and the capture rate with animal, plant and unknown items, respectively. The dependent variables were the group means of the group members that had taken at least one item to the nest.

Results

No association existed between brood size and habitat (χ^2= 0.06, df= 2, P = 0.97). The median brood size was three in both habitats. Neither group size (Mann-Whitney-U test, N= 49, Z= 0.357, P= 0.72) nor the proportion of groups with helpers differed between habitats (χ^2= 0.164, df= 1, P> 0.05). In the suburban habitat, 18 groups had helpers and seven groups had no helpers; in the wildland, 16 groups had helpers and 8 groups had no helpers.

Food capture rates and foraging patch selection: In the suburbs a greater proportion of plant items was captured than in the wildlands (Figure 1, one-way ANOVA, $F_{1, 46}$= 6.189, P= 0.02). Table 1 shows the composition of items captured in both habitats. Suburban groups foraged more efficiently than wildland groups in both human-modified and unaltered native patches capturing animal, plant, and unknown food items at higher rates than wildland groups (Figure 2a, Mann-Whitney-U tests, N= 49, animal items: Z= -1.92, P= 0.06, plant items: Z = -2.46, P= 0.01, unknown items: Z= - 2.99, P< 0.01). In unaltered native patches only, suburban groups captured animal and unknown foods at an equal rate and plant foods at a higher rate than wildland groups (Figure 2: compare wildland in 2a, with suburban unaltered in 2b; Mann-Whitney-U test, N= 48, animal items: Z= 1.406, P= 0.16, plant items: Z=-2.37, P= 0.01, unknown items: Z= 0.00, P= 1.00). Within the suburbs (Figure 2b), the capture rate of animal items were similar in human-modified and unaltered native patches, while the capture rates of plant items and of unknown items, respectively, were higher in human-modified patches than in unaltered native patches (Wilcoxon signed-rank tests, N= 22, animal items: S= 11.0, P= 0.68, plant items: S= -84.5, P< 0.01, unknown items: S= -62.5, P< 0.01).

The median proportion of human-modified patches within suburban territories was 0.353, (N= 25, interquartile range [IQR]: 0.241 - 0.436), but suburban birds spent 39% percent of their time foraging in human-modified patches, suggesting some preference (median of 0.387, IQR= 0.166 - 0.683; Wilcoxon signed-rank test, S= 104.5, N= 25, P< 0.01) over unaltered native patches.

Parental time budget: The proportion of time pairs spent in territorial behavior did not differ between the habitats (median + IQR, suburban: 0.01, 0.00 - 0.01, wildland: 0.01, 0.00 - 0.01, Mann-Whitney-U test, N= 49, Z= -0.576, P= 0.564). Suburban pairs visited the nest at equal rates (median + IQR, suburban: 1.00, 0.5 – 1.5, wildland: 0.66, 0.33 – 1.25,

Mann-Whitney-U test, N= 49, Z= -0.94, P= 0.35) but spent more time on the nest and an equal amount of time on sentinel compared to wildland pairs (Figure 3a and b, Table 2). Suburban pairs foraged less (Figure 3c) but did not find fewer animal items or a decreased total number of items per observation hour than wildland pairs (animal items: Mann-Whitney-U test, N= 49, Z= -0.341, P= 0.733; total number of items: Table 2d, Figure 3d).

The presence of helpers did not influence the time pairs spent on the nest or on sentinel (Table 2a and b). Suburban pairs with helpers foraged less than those without helpers, but the opposite pattern occurred in the wildland habitat (Table 2c, significant habitat × presence of helpers interaction). Suburban and wildland helpers did not differ in the time spent in territorial behavior, on sentinel, on the nest, foraging, total number of items found, the number of items taken to the nest and the proportion of plants taken to the nest (Mann-Whitney-U test, N= 15; territorial behavior: Z= 0.896, P= 0.39, on the nest: Z= 1.434, P= 0.15, on sentinel: Z= 0.295, P= 0.77, foraging: Z= -0.413, P= 0.68, number items found: Z= 0.00, P= 1.00, number of items taken to nest: Z= 1.662, P= 0.09, proportion of plant items taken to nest: N= 4, Z= 0.00, P= 1.00).

Because suburban females spent more time on the nest and less time foraging than wildland females a significant interaction existed between habitat and sex in these two behaviors (Figure 3, Table 2a and c, habitat × sex interactions). In addition, suburban females allocated more time to being on the nest, less to foraging and being on sentinel and also captured fewer items per observation hour than suburban males (Figures 3d, Table 2d). Wildland females spent more time on the nest than wildland males, but the difference was smaller than in the suburban habitat (Figure 3a). Furthermore, wildland females did not differ from their mates in the time they allocated to foraging and being on sentinel and in the number of items found per observation hour (Figure 3b and c).

Nestling diet: In both habitats the proportion of plant items captured was higher than the proportion of plant items taken to the nest (Figure 1, Wilcoxon signed-rank tests; suburban: N= 20, S= 72.5, P< 0.01, wildland: N= 16, S= 60.0, P< 0.01). Nestling diet differed between habitats: in the suburbs, on average roughly 13% of all the plant items captured (N= 191) were taken to the nest, while in the wildland, 0% of the plant items (N= 53) captured were brought to nestlings (Figure 1, Mann-Whitney-U test, Z= 88, N= 36, P< 0.01). In the suburbs, the plant items captured were 124 human-provided items and 40 acorns, and the plant items taken to the nest were 13 human-provided items and 3 acorns. In

the wildland, plant items captured consisted of 7 human-provided items and 41 acorns. This suggests partial preference for plant items in the suburbs, but not in the wildland. Suburban jays were as likely to take human-provided foods to the nest as acorns (χ^2= 1.255, N= 189, P> 0.05). No difference existed between suburban groups that took plant items to the nest (N= 9) and those suburban groups that delivered only animal items (N= 11) in the frequency of helper presence (1 out of 9 groups, 1 out of 11 groups, respectively, χ^2= 0.448, P> 0.05), brood size (Mann-Whitney-U test, Z= 0.558, P= 0.573) and the time spent foraging (Mann-Whitney-U test, Z= 0.304, P= 0.76). Capture rates for animals, plants and unknown items did not differ between groups taking plant items to the nest and those not taking plant items to the nest either (median + IQR plants to nest / no plants to nest, animals: 0.70, 0.55 – 1.12 / 0.82, 0.53 – 2.00, Mann-Whitney U-Test, Z = -0.68, P= 0.49, plants: 0.69, 0.38 - 1.17 / 0.31, 0.13 – 0.54, Z= 1.48, P= 0.14, unknown items: 0.30, 0.21 – 0.69 / 0.43, 0.19 - 0.89, Z = -0.15, P= 0.88). Thus, according to my predictions, more plant items were delivered to the nest in the suburban than in the wildland habitat, and in both habitats, birds brought fewer plant items to the nest than they captured, suggesting preference for animal foods when feeding nestlings.

Discussion

My results supported only the last of the five hypotheses tested. I found that suburban adults brought approximately 15% human-provided foods to the nestlings, but wildland parents fed nestlings exclusively animal foods. However, suburban parents do not appear to feed plant foods to their nestlings because animal foods are limited: suburban groups captured animal food items at a higher rate than wildland groups. Contrary to my expectations, human-modified patches were profitable sites for animal foods. Suburban groups foraged preferentially in human-modified patches and captured animal foods at an equal rate and plant food at a higher rate than in unaltered native patches. In addition, suburban pairs captured a similar number of animal and more plant items per observation hour than wildland pairs despite foraging less. Suburban pairs spent more time on the nest than wildland pairs, but not in other defense behaviors. Thus, suburban birds do not appear to be limited by time for foraging or by the availability of arthropods, thus neither time nor food limitations appears to be an adequate explanation for the inclusion of plant foods in the diet of suburban nestlings.

Although Florida scrub-jays mostly fed animal foods to their nestlings in both habitats, suburban birds regularly delivered plant foods to the nestlings. However, they carried fewer plant items to the nest than they captured, which is an example of partial preference for plant foods. Partial preference for a food type is generally defined as when this food type is sometimes taken and sometimes ignored when captured (Berec and Krivan 2000). Classic optimal foraging models predict that a food type is always included or rejected (e.g. Stephens and Krebs 1986). Several authors have expanded the classic models (for references see Berec and Krivan 2000) and propose several mechanisms leading to partial preference. The partial preference for plants in the diet of suburban nestlings that I found might be explained by the following four mechanisms: (1) the capture rate with the less preferred food type influences diet choice (Houston 1985); (2) observers or foragers estimate the profitability of the prey types incorrectly (McNamara and Houston 1987); (3) foragers know only the local food availability, not the overall food availability (Berec and Krivan 2000); and (4) foragers respond more to recent than to past events (Hirvonen et al. 1999, Berec and Krivan 2000). None of the four mechanisms requires time or energy limitation of the parents. The first mechanism was predicted by Houston (1985), who modeled choice between two prey types for a central place forager. In the model, the higher the capture rate with the less preferred food relative to the preferred food, the greater the proportion of the less preferred food in the nestling diet. My results agree with this model. Plant foods, especially human-provided foods, were fed to nestlings in the suburban but not in wildland habitat and the capture rate of plant foods was much higher in the suburban habitat, likely because human-provided food is ubiquitous. This result indicates that there might be a threshold plant-animal ratio above which birds take plant items to the nest as predicted by the optimal diet model (Stephens and Krebs 1986). In addition, not all suburban groups fed their nestlings plants. Those that did, captured plants at approximately twice the rate than those that delivered only animal items, however the differences was not significant probably because of the low sample size.

The second mechanism predicts that discrimination errors lead to partial preference (McNamara and Houston 1987). I assumed that human-provided foods and other plant foods are of equal quality and that arthropods do not differ in nutritional quality between the habitats. However, human-provided plant foods might be of higher quality than other plant foods. Peanuts, the most common human-provided food in the suburban habitat, have

more than twofold higher protein and fat content than acorns (USDA 2005), the most common plant food in the wildland. In addition, acorns are protected by non-digestible tannins (Fleck 1988). Alternatively, nestlings might have a reduced ability to digest plant foods (Karasov and Wright 2002), and jays might incorrectly perceive peanuts as high quality for nestlings. In support, jays seemed to perceive peanuts as higher quality than other plant foods in a previous experimental study (Sauter et al. unpublished, chapter 3), which was not the case here. I might not have detected an existing preference in this study, because wildland parents found very few human-provided items and suburban parents captured few acorns. Alternately, suburban parents may exhibit a partial preference for plant foods because the quality of the arthropods captured in the suburbs is inferior to those in the wildlands. Shawkey et al. (2004) reported that the abundance of lepidopteran larvae and orthopterans, the primary foods in the diet of nestlings, is lower in native habitat patches in the suburbs than in the wildlands. For most items observed in this study, I could only specify if they were animal or plant, therefore, I do not know whether the quality of the animal food captured in the suburbs is inferior to the wildlands. Hence, discrimination errors could cause the partial preference detected in my study.

The third and fourth mechanisms predict partial preference a) when local capture rates with the preferred foods are lower than the average capture rate in the environment, b) when local capture rate with the less preferred food is higher than the average capture rate in the environment, or c) when both a) and b) are true. Human-provided food sources, such as bird feeders or people feeding the jays directly, offer a spatially and/or temporally high abundance of low-quality food for nestlings. Thus in suburban habitats, where human-provided food is abundant and arthropods are less abundant than in wildlands, the local capture rate with the less preferred food is higher and with the preferred food is lower than the average capture rates with these food types in their environment. Hence, jays might show a partial preference when visiting human-provided food sources. In support, suburban groups that took plant items to the nest had higher capture rates with plant foods and lower capture rates with animal foods than suburban groups delivering animal foods exclusively, even though these differences were not statistically significant. In addition, in a previous experiment we increased peanut capture rates and subsequently observed wildland parents feeding some peanuts to their nestling (Sauter et al. unpublished, chapter 3).

Partial preference for the less preferred food also may be caused by food limitation of the parents (Wright et al. 1998). However, I found that suburban parents were more efficient foragers than wildland birds and, therefore, did not appear to be food limited. Long-term demographic studies also support a lack of food limitation in suburban adults (Bowman et al. submitted). As a consequence of the access to human-provided foods, suburban birds breed earlier and lay larger clutches than wildland birds. My study did not support Shochat (2004) who suggested that, although food abundance may be higher in urbanized areas than in native areas, food may be a limiting factor for foraging at the individual level.

My finding that in native vegetation suburban birds tend to have a higher foraging efficiency for animal foods than do wildland birds does not agree with a previous study showing lower abundance of arthropods in unaltered native patches within suburban habitat than in wildland vegetation (Shawkey et al. 2004). The two studies disagree, because foraging efficiency is expected to depend on the amount of food available (Zanette et al. 2000). One explanation for the disagreement may be that natural foods are more clumped in space in the suburbs than in the wildlands because more habitat edge occurs in the suburban habitat (Bowman et al. submitted). Edges can have a higher arthropod abundance than the surrounding habitat (Dangerfield et al. 2003). Hence, suburban foragers might forage more efficiently for animal foods. In addition, suburban parents might exploit only the habitat patches with the highest abundance of arthropods when foraging for animal food. Suburban parents probably need less animal foods than wildland parents, because they can fulfill their own nutritional needs with human-provided foods.

Suburban parents were more efficient foragers than wildland parents, and thus, they were unlikely to be time-limited for foraging. In addition, suburban parents did not spend more time in territorial behaviors and on sentinel than wildland parents did as I expected. In contrast to pre-breeding, when suburban females were engaged in more inter-specific interactions than wildland females (Fleischer et al. 2003). I found no difference in the time allocated to this behavior between the habitats, probably because jays spend more time in territorial interactions pre-breeding when they reestablish their breeding territories and do not have to provide young (pers. observation). However, even pre-breeding the time spent in inter-specific interactions was not more than 0.5 % in suburban females (Fleischer et al. 2003). Suburban pairs attended the nest more than wildland pairs, perhaps because they

were freed from spending more time foraging or because the perceived an increased need to defend their nest (Hailman and Woolfenden 1985). However, increased time spent on the nest was not associated with decreased foraging success, i.e. fewer animal or plant items found per observation hour. Therefore, I found no evidence that elevated investment in defense behavior leads to time limitation for foraging. In addition, my results give little support for suburban pairs being time limited for foraging because they lack helpers. Although the presence of helpers was associated with a decrease in foraging time of the suburban pairs, helper presence did not relate to the number of items found by the pair. Furthermore, in the suburbs the same proportion of families had helpers than in the wildland and helpers did not differ in time budgets, foraging efficiency and the amount and composition of items taken to the nest between the habitats. Suburban females caused the increased nest attendance of suburban pairs, as they sat more on the nest than wildland females. This shift in behavior could be costly, if it incurs higher female mortality (Slagsvold and Dale 1996). Hence, the reasons and consequences of being on the nest longer need further study.

In summary, I found that neither food nor time limitation explains why suburban Florida scrub-jays feed human-provided foods to nestlings and wildland jays do not. Even though I do not know the effect of the human-provided foods on Florida scrub-jay nestling fitness, other studies have found that feeding low-quality human-provided foods to nestlings decreases reproductive success (Belant et al. 1998, Boal 1999, Annett and Pierrotti 1999). Human-provided food sources are generally clumped in space and/or time (Annett and Pierrotti 1999), and therefore provide locally and/or temporally more abundant foods than the average abundance in the environment. Therefore, many urban species may feed human-provided foods to nestlings despite a lack of food limitation, if exploiting human-provided food sources causes partial preference for these low quality foods. This study suggests that partial preferences maybe caused by an increased encounter rate with the less preferred food.

Acknowledgements

I thank R. Bowman and G. Woolfenden for access to their study populations and demographic data. This manuscript benefited from the comments of R. Bowman, G. Pasinelli and S.J. Reynolds. L. Kearns, S. LeClair, J. Michalak and S.Wagner mapped the

territories and G. Pasinelli digitized the habitat patches. I was supported by a graduate research internship at Archbold Biological Station, and by the American Ornithologists' Union, Basler Stiftung für biologische Forschung, DeGiacomi Foundation, Florida Ornithological Society, Janggen-Pöhn Foundation, Roche Research Foundation, and Wolfermann-Nägeli Foundation. Research in the suburban and wildland sites was supported by NSF grants IBN-0077469 and -0346557 to Reed Bowman. All research on this listed species was permitted by the US Fish and Wildlife Service (permit TE824723-5 to Reed Bowman).

References

Abrahamson, W. G., A. F. Johnson, J. N. Layne, and P. A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. Florida Scientist **47**:209-250.

Annett, C. A., and R. Pierrotti. 1999. Long-term reproductive output in Western gulls: consequences of alternate tactics in diet choice. Ecology **80**:288-297.

Aparicio, J. M., and R. Bonal. 2002. Effects of food supplementation and habitat selection on timing of Lesser Kestrel breeding. Ecology **83**:873-877.

Belant, J. L., S. K. Ickes, and T. W. Seamans. 1998. Importance of landfills to urban-nesting herring and ring-billed gulls. Landscape and Urban Planning **43**:11-19.

Berec, L., and V. Krivan. 2000. A mechanistic model for partial preference. Theoretical Population Biology **58**:279-289.

Birkhead, T. R., F. Fletcher, and E. J. Pellatt. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. Proceedings of the Royal Society of London Series B **266**:385-390.

Blanckenhorn, W. U. 1991. Fitness consequences of foraging success in water striders (*Gerris remigis*; Heteroptera: Gerridae). Behavioral Ecology **2**:46-55.

Boal, C. W., and R. W. Mannan. 1999. Comparative breeding ecology of Cooper's Hawks in urban and exurban areas of southeastern Arizona. Journal of Wildlife Management **63**:77-84.

Boutin, R. B. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. Canadian Journal of Zoology **68**:203-220

Bowman, R., and G. E. Woolfenden. 2001. Nest success and the timing of nest failure of Florida scrub-jays in suburban and wildland habitats. Pages 383-402 *in* J. M. Marzluff, R. Bowman, and R. E. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, New York.

Bowman, R., and G. E. Woolfenden. 2002. Nest site selection by Florida scrub-jays in natural and human-modified habitats. Wilson Bulletin **114**:128-135.

Bowman, R., G. E. Woolfenden, and J. W. Fitzpatrick. submitted. Timing of breeding and clutch size in Florida Scrub-Jays across an urban gradient in South-Central Florida. Conservation Biology.

Bowers, M. A., and B. Breland. 1996. Foraging of gray squirrels on an urban-rural gradient: Use of the GUD to assess anthropogenic impact. Ecological Applications **6**:1135-1142.

Breininger, D. R. 1999. Florida Scrub-Jay Demography and Dispersal in a Fragmented Landscape. Auk **116**:520-527.

Clergeau, P., J. P. L. Savard, G. Mennechez, and G. Falardeau. 1998. Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. Condor **100**:413-425.

Dangerfield, J. M., A. J. Pik, D. Britton, A. Holmes, M. Gillings, I. Oliver, D. Briscoe, and A. J. Beattie. 2003. Patterns of invertebrate biodiversity across a natural edge. Austral Ecology **28**:227-236.

DeGange, A. R. 1976. The daily and annual time budget of the Florida scrub-jay. M. Sc. thesis, University of South Florida, Tampa.

Dickman, C. R., and C. P. Doncaster. 1987. The ecology of small mammals in urban habitats. II. Demography and dispersal. Journal of Animal Ecology **58**:119-127.

Dosch, J. J. 1997. Diet of nestling Laughing gulls in Southern New Jersey. Colonial Waterbirds **20**:273-281.

Fernandez-Juricic, E., and J. L. Telleria. 2000. Effects of human disturbance on spatial and temporal feeding patterns of Blackbird Turdus merula in urban parks in Madrid, Spain. Bird Study **47**:13-21.

Fedriani, J. M., T. K. Fuller, and R. M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography **24**:325-331.

Fleck, D.C. 1988 Acorn tannin influences on the caching behavior of the Florida Scrub Jay (*Aphelocoma c. coerulescens*) M.Sc. thesis, University of South Florida, Tampa.

Fleischer, A. L., R. Bowman, and G. E. Woolfenden. 2003. Variation in foraging behavior, diet and the time of breeding of Florida Scrub-Jays in suburban and wildland habitats. Condor **105**:515-527.

Francis, A. M., J. P. Hailman, and G. E. Woolfenden. 1989. Mobbing by Florida scrub jays: behaviour, sexual asymmetry, role of helpers and ontogeny. Animal Behaviour **38**:795-816.

French, K., R. Major, and K. Hely. 2005. Use of native and exotic garden plants by suburban nectarivorous birds. Biological Conservation **121**:545-559.

Hailman, J. P., and G. E. Woolfenden. 1985. Nest-defense of the Florida scrub-jay and the problem of "incubation" by male passerines. Wilson Bulletin **97**:370-372.

Hirvonen, H., E. Ranta, H. Rita, and N. Peuhkuri. 1999. Significance of memory properties in prey choice decisions. Ecological Modelling **115**:177-189.

Houston, A. I. 1985. Central place foraging: some aspects of prey choice for multiple-prey loaders. American Naturalist **125**:811-826.

Johnston, R. D. 1993. Effects of diet quality on the nestling growth of a wild insectivorous passerine, the House Martin *Delichon urbica*. Functional Ecology **7**:255-266.

Karasov, W. H., and J. Wright. 2002. Nestling digestive physiology and begging. Pages 199-219 *in* J. Wright and M. L. Leonard, editors. The evolution of begging: competition, cooperation and communication. Kluwer Academic Publishers, Dordrecht, Netherlands.

Markman, S., B. Pinshow, and J. Wright. 2002. The manipulation of food resources reveals sex-specific trade-offs between parental self-feeding and offspring care. Proceedings of the Royal Society of London Series B **269**:1931-1938.

Martin, P., and P. Bateson. 1986. Measuring behavior. Cambridge University Press, Cambridge, NY.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19-48 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwall, MA.

McIntyre, N. E. 2000. Ecology of urban arthropods: A review and a call to action. Annals of the Entomological Society of America **94**:825-835.

McNamara, J., and A. I. Houston. 1987. Partial preferences and foraging. Animal Behaviour **35**:1084-1099.

Mumme, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. Behavioral Ecology and Sociobiology **31**:319-328.

Schoech, S. J., and R. Bowman. 2003. Does differential access to protein influence differences in timing of breeding of Florida Scrub-Jays (*Aphelocoma coerulescens*) in suburban and wildland habitats? Auk **120**:1114-1127.

Schoech, S. J., R. L. Mumme, and J. C. Wingfield. 1996. Prolactin and helping behaviour in the cooperatively breeding Florida scrub-jay, *Aphelocoma c. coerulescens*. Animal Behaviour **52**:445-456.

Shawkey, M. D. 2001. Proximate causes of brood reduction in Florida Scrub-Jays. M. Sc. thesis. University of South Florida, Tampa.

Shawkey, M. D., R. Bowman, and G. E. Woolfenden. 2004. Why is brood reduction in Florida scrub-jays higher in suburban than in wildland habitats? Canadian Journal of Zoology **82**:1427-1435.

Shochat, E. 2004. Credit or debit? Resource input changes population dynamics of city-slicker birds. OIKOS **106**:622-626.

Shochat, E., S. B. Lerman, M. Katti, and D. B. Lewis. 2004. Linking optimal foraging behavior to bird community structure in an urban-desert landscape: Field experiments with artificial food patches. American Naturalist **164**:232-243.

Slagsvold, T., and S. Dale. 1996. Disappearance of female pied flycatchers in relation to breeding stage and experimentally induced molt. Ecology **77**:461-471.

Stallcup, J. A., and G. E. Woolfenden. 1978. Family status and contributions to breeding by Florida Scrub Jays. Animal Behaviour **26**:1144-1156.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.

USDA. 2005. USDA Nutrient Database. U.S. Department of Agriculture, http:/www. nal.usda.gov/fnic/foodcomp/.

Woolfenden, G. E., and J. W. Fitzpatrick. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird. Princeton University Press, Princeton, New Jersey.

Woolfenden, G. E., and J. W. Fitzpatrick. 1996. Florida Scrub-Jay *(Aphelocoma coerulescens)*. Pages 1-28 *in* A. Poole, editor. The Birds of North America. American Ornithologists' Union and The Academy of Natural Sciences, Philadelphia.

Wright, J., C. Both, P. A. Cotton, and D. Bryant. 1998. Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. Journal Of Animal Ecology **67**:620-634.

Zanette, L., P. Doyle, and S. M. Tremont. 2000. Food shortage in small fragments: Evidence from an area-sensitive passerine. Ecology **81**:1654-1666.

Table 1: Composition of captured items in the suburban and wildland habitat. N = total number of items captured.

	Suburbs			Wildlands
Food item	unaltered native (N = 195) [%]	human-modified (N = 493) [%]	unknown (N = 162) [%]	N =1172 [%]
Animal total	**72**	**34**	**40**	**48**
Unidentified animals	52	22	22	30
Insecta	4	5	7	7
Formica		4	1	
Vespidae (including larvae pulled from a wasp nest)	3		9	< 1
Lepidopteran larvae	7		1	4
Other larvae	1	< 1		4
Arachnidea (including egg cases)	2		1	< 1
Vertebrates	1			2
Phasmatidae				1
Orthoptera	< 1	< 1		1
Lumbricus		< 1		
Odonata	< 1	< 1		< 1
Coleoptera				< 1
Plant total	**9**	**25**	**14**	**10**
Unidentified plants	2	2	4	1
Human-provided (seeds, bread,peanuts)	3	19		1
Acorns	4	4	10	7
Berries				2
Unknown items	**19**	**41**	**46**	**42**

Table 2: The effects of habitat, sex, brood size and presence of helpers (no/yes) on a) proportion of time spent on nest, b) proportion of time spent on sentinel, c) proportion of time spent foraging, and d) number of items found per observation hour by breeding Florida scrub-jay pairs. Results of mixed model analyses (see methods). N = 49 pairs.

		a) on nest		b) on sentinel		c) foraging		d) number of items found per observation hour	
source	df	F	P ≤	F	P ≤	F	P ≤	F	P ≤
habitat	1	18.30	0.001	0.66	0.420	19.38	0.001	4.25	0.045
sex	1	47.78	0.001	17.75	0.001	15.46	0.001	8.04	0.007
brood size	1	0.11	0.754	0.77	0.385	2.61	0.113	5.58	0.027
presence of helpers	1	0.59	0.448	0.08	0.774	0.00	0.946	0.09	0.770
habitat × sex	1	8.75	0.005			8.57	0.005	14.33	0.001
habitat × presence of helpers	1					5.11	0.029		

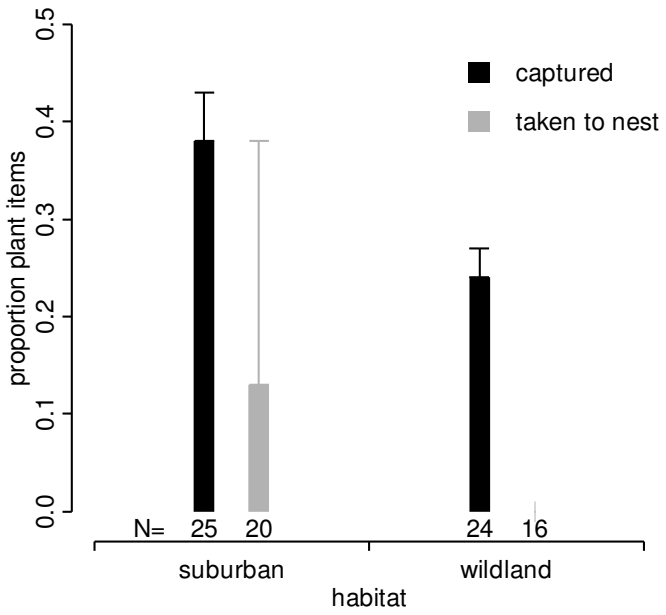

Figure 1: Mean proportion (± SE) of plant items captured and taken to the nest in relation to habitat.

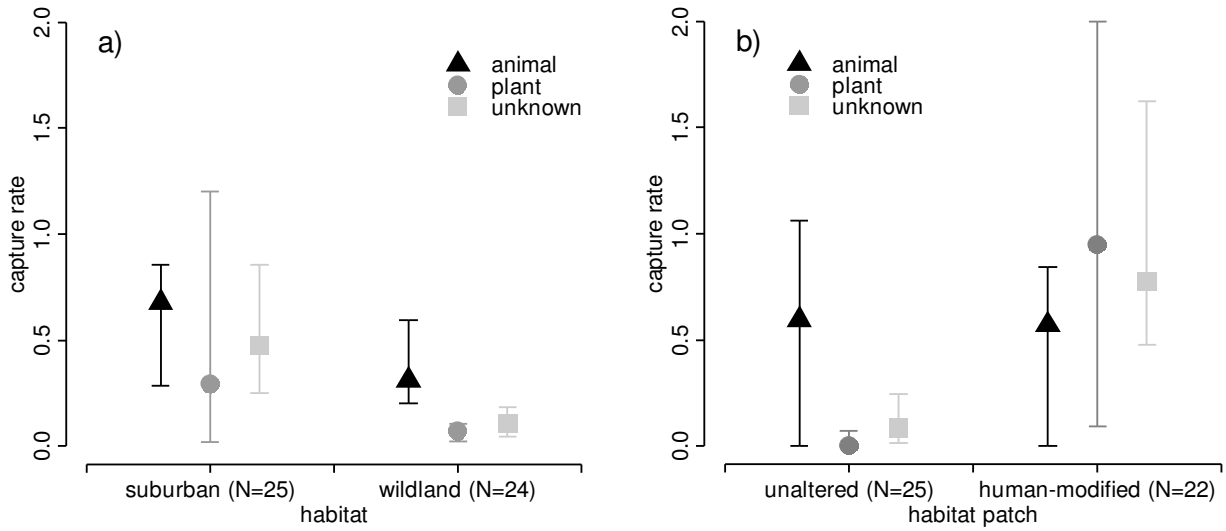

Figure 2: Medians and inter-quartile ranges of the capture rates (items found per foraging minute) per group of animal, plant, and unknown items a) in suburban versus wildland habitat, b) in the suburban habitat in unaltered versus human-modified habitat patches. N = number of groups.

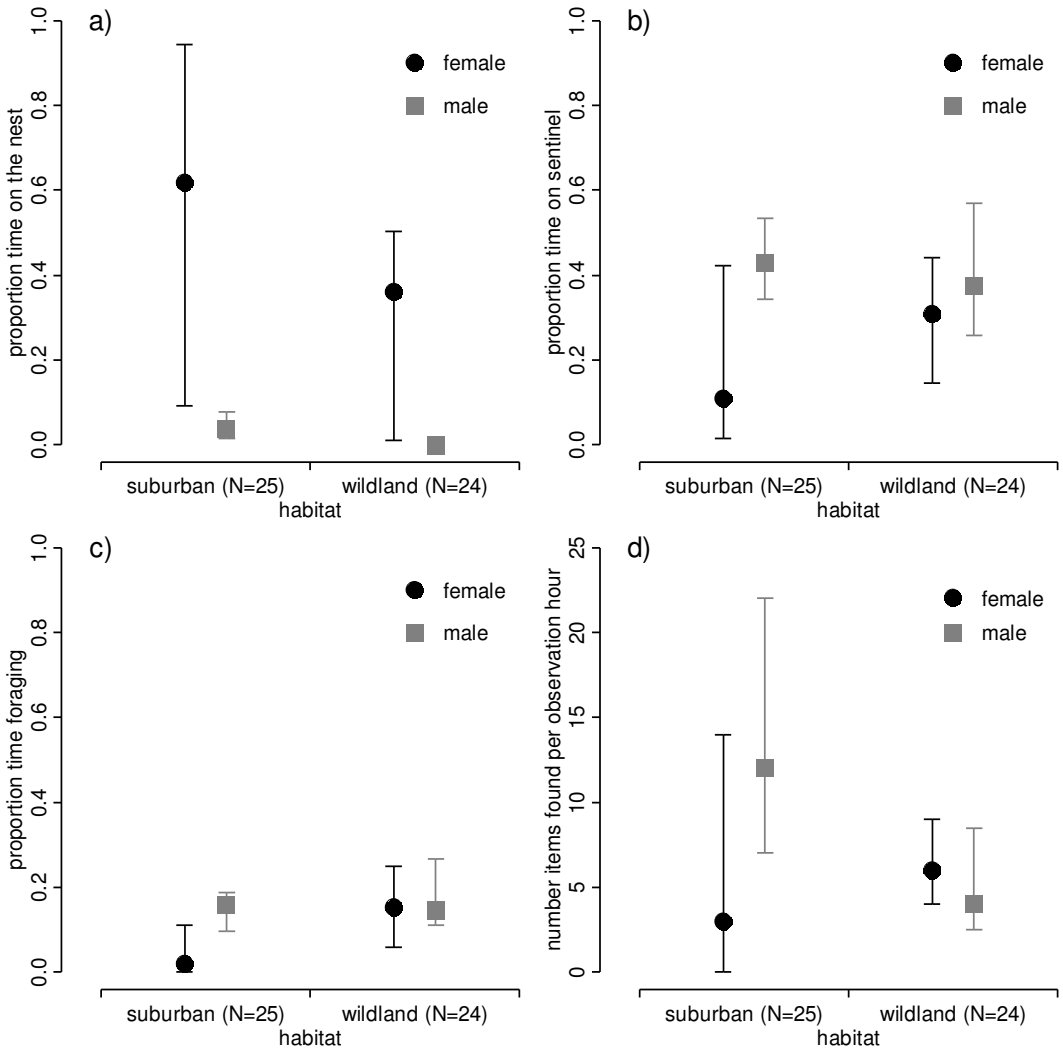

Figure 3: Medians and inter-quartile ranges of the proportion of time spent a) on nest, b) on sentinel, c) foraging by pairs and d) total number of items found per observation hour in relation to habitat

CURRICULUM VITAE

Name	Sauter
First name	Annette
Birth	24. April 1974
Citizenship	Ermatingen Thurgau

Education

1990 - 1995	Kantonsschule Romanshorn, Maturität Typus B
1992	Exchange student in Chile
1995 - 2000	Studied Biology at the University of Zurich

Diploma in	Zoology
Title of the diploma thesis	The mating plug as a chastity belt in a bumblebee
At the University of Zurich since	October 1995, PhD student since October 2001

Publications

Sauter, A. & Brown, M.J.F. (2001): To copulate or not? The importance of female status and behavioural variation in predicting copulation in a bumblebee. Animal Behaviour 62: 221-226

Sauter, A., Brown, M. J. F., Baer, B., & Schmid-Hempel, P. (2001): Males of social insects can prevent females from multiple mating. Proceedings of the Royal Society of London Series B 268: 1449-1454

Grants and awards

Grants for material expenses from the American Ornithologists' Union, Florida Ornithological Society and Stiftung deGiacomi: CHF 7'000, 2003

Travel grants from the American Ornithologists' Union, Basler Stiftung für biologische Forschung and the Swiss Zoological Society: CHF 5'100, 2003-2004

Grants for living costs during my PhD from the Basler Stiftung für biologische Forschung, Janggen-Poehn Stiftung, Roche Research Foundation and Wolfermann Nägeli Stiftung: CHF 92'000, 2002-2005

Grant from the Deutsche Forschungsgesellschaft for the graduate program "Perception and management of biodiversity" at the University of Göttingen, Germany, 2000